UNIVERSIDADE FEDERAL DO PARANÁ

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DETERMINANTES DAS INTERAÇÕES E A DIVERSIDADE FUNCIONAL DE PARCEIROS DE ESPÉCIES CENTRAIS EM UMA REDE DE DISPERSÃO DE SEMENTES POR AVES DA MATA ATLÂNTICA

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Tese apresentada ao curso de Pós-Graduação em Ecologia e Conservação, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial à obtenção do título de Doutor em Ecologia e Conservação.

Orientadora: Profa. Dra. Isabela Galarda Varassin

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TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná foram convocados para realizar a arguição da tese de Doutorado de **TIAGO MACHADO DE SOUZA** intitulada: **DETERMINANTES DAS INTERAÇÕES E A DIVERSIDADE FUNCIONAL DE PARCEIROS DE ESPÉCIES CENTRAIS EM UMA REDE DE DISPERSÃO DE SEMENTES POR AVES DA MATA ATLÂNTICA**, após terem inquirido o aluno e realizado a avaliação do trabalho, são de parecer pela sua APROVAÇÃO no rito de defesa.

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Curitiba, 28 de Março de 2018.

ISABELA GALARDA VARASSIN
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ATA Nº12

ATA DE SESSÃO PÚBLICA DE DEFESA DE DOUTORADO PARA A OBTENÇÃO DO GRAU DE DOUTOR EM ECOLOGIA E CONSERVAÇÃO

No dia vinte e oito de março de dois mil e dezoito às 14:00 horas, na sala Secretaria PPGECO, Setor de Ciências Biológicas, foram instalados os trabalhos de argulção do doutorando **TIAGO MACHADO DE SOUZA** para a Defesa Pública de sua tese intitulada **DETERMINANTES DAS INTERAÇÕES E A DIVERSIDADE FUNCIONAL DE PARCEIROS DE ESPÉCIES CENTRAIS EM UMA REDE DE DISPERSÃO DE SEMENTES POR AVES DA MATA ATLÂNTICA**. A Banca Examinadora, designada pelo Colegiado do Programa de Pós-Graduação em ECOLOGIA E CONSERVAÇÃO da Universidade Federal do Paraná, foi constituída pelos seguintes Membros: ISABELA GALARDA VARASSIN (UFPR), MARCOS BERGMANN CARLUCCI (UFPR), JEFERSON VIZENTIN BUGONI (UNICAMP), MARCO AURÉLIO PIZO (UNESP/RC), PAULO ROBERTO GUIMARAES JUNIOR (null). . Dando início à sessão, a presidência passou a palavra ao discente, para que o mesmo expusesse seu trabalho aos presentes. Em seguida, a presidência passou a palavra a cada um dos Examinadores, para suas respectivas arguições. O aluno respondeu a cada um dos arguidores. A presidência retomou a palavra para suas considerações finais. A Banca Examinadora, então, reuniu-se e, após a discussão de suas avaliações, decidiu-se pela APROVAÇÃO do aluno. O doutorando foi convidado a ingressar novamente na sala, bem como os demais assistentes, após o que a presidência fez a leitura do Parecer da Banca Examinadora. A aprovação no rito de defesa deverá ser homologada pelo Colegiado do programa, mediante o atendimento de todas as indicações e correções solicitadas pela banca dentro dos prazos regimentais do programa. A outorga do título de doutor está condicionada ao atendimento de todos os requisitos e prazos determinados no regimento do Programa de Pós-Graduação. Nada mais havendo a tratar a presidência deu por encerrada a sessão, da qual eu, ISABELA GALARDA VARASSIN, lavrei a presente ata, que vai assinada por mim e pelos membros da Comissão Examinadora.

Curitiba, 28 de Março de 2018.

ISABELA GALARDA VARASSIN
Presidente da Banca Examinadora

MARCOS BERGMANN CARLUCCI
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PAULO ROBERTO GUIMARAES JUNIOR
Avaliador Externo

Dedico esta tese à minha esposa Ana Camila, aos meus filhos Raul e João, aos meus avós, em especial ao Rogério e Legri (*in memoriam*), aos meus pais Sergio e Amarilda, aos meus irmãos e irmãs e a todas as pessoas que fizeram parte do desenvolvimento desta tese.

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RESUMO

A dispersão de sementes é amplamente reconhecida como uma função ecológica chave apresentando um papel importante na manutenção do funcionamento dos ecossistemas. Estudos sobre redes de dispersão de sementes, bem como sobre outras redes mutualísticas, têm apresentado propriedades estruturais semelhantes como baixa conectância, estrutura aninhada e distribuição assimétrica das interações. Dois processos têm sido considerados como determinantes destas propriedades estruturais. O conceito de processos neutros considera as abundâncias das espécies como determinantes da estrutura das redes e frequência de encontro entre espécies. Por outro lado, o conceito de processos relacionados ao nicho presume que as estruturas das redes são moldadas por restrições nas interações (e.g. ausência de sobreposição espacial, temporal e barreiras morfológicas nas interações) Dado o pouco conhecimento sobre a importância relativa destes processos na estrutura de redes de dispersão de sementes, no primeiro capítulo desta tese nós avaliamos a importância relativa de processos neutros e relacionados ao nicho em predizer a estrutura (conectância, aninhamento, aninhamento ponderado, uniformidade das interações e especialização complementar) de uma rede de dispersão de sementes, assim como em predizer as interações par a par entre as espécies (i.e. microestrutura). Como resultado, ambos os processos predisseram a conectância e aninhamento. No entanto, o aninhamento foi influenciado principalmente pelos processos neutros. A sobreposição temporal entre plantas com frutos maduros e a presença das aves, como um processo relacionado ao nicho, foi o modelo mais parcimonioso capaz de predizer as frequências das interações par a par. Além das propriedades estruturais conservadas em redes mutualísticas, estudos também mostraram que em redes ecológicas diferentes espécies podem ter diferentes papéis dentro da rede. Dentre estes papéis, a centralidade das espécies é um dos mais importantes, uma vez que espécies centrais são responsáveis por manter a estrutura e estabilidade em redes ecológicas. No entanto, a relevância das espécies centrais para a manutenção da diversidade funcional em redes ecológicas permanece pouco conhecida. Assim, o segundo capítulo desta tese apresenta o conceito de diversidade funcional de parceiros em redes ecológicas. Nós avaliamos a relação entre a diversidade funcional de parceiros e a centralidade de aves em uma rede de dispersão de sementes da Mata Atlântica. Adicionalmente, nós também avaliamos os fatores determinantes da centralidade das aves. Nós encontramos uma forte correlação entre a diversidade funcional de parceiros e a centralidade das aves, independente das suas relações filogenéticas. Em relação aos fatores determinantes da centralidade das aves, a abundância das espécies apresentou o maior poder de explicação, seguido pelo nível de frugivoria e forrageamento no solo. Portanto, este capítulo mostrou que aves centrais em uma rede de dispersão de sementes também são importantes para a manutenção da diversidade funcional de plantas. Por fim, os resultados desta tese destacam a importância de processos neutros e relacionados ao nicho em predizer a estrutura e interações entre as espécies em uma rede de dispersão de sementes, bem como em determinar a centralidade de aves dispersoras, a qual está diretamente relacionada com a diversidade funcional de plantas com as quais elas interagem.

Palavras-chave: abundância, atributos funcionais, centralidade, diversidade funcional, estrutura de redes, frugivoria, Mata Atlântica, processos neutros, processos relacionados ao nicho, redes mutualísticas

ABSTRACT

Seed dispersal is widely recognized as a key ecological function, playing an important role in maintaining the structure and functioning of ecosystems. Studies on seed dispersal networks, as well as on other mutualistic networks, have shown similar structural properties such as low connectance, nested structure and asymmetric distribution of interactions. Two processes have been considered as determinants of these structural properties conserved in mutualistic networks. The concept of neutral processes considers the abundance of species as determinants of the structure of the networks and frequency of encounter between species. On the other hand, the concept of niche-related processes assumes that network structures are shaped by constraints to interactions (e.g. absence of spatial, temporal overlap and morphological barriers in interactions). Given the little knowledge about the relative importance of these processes in the structure of interactions seed dispersion networks, the first chapter of this thesis evaluated the combined ability of neutral and niche-based processes to predict the structure (connectance, nestedness, weight nestedness, interaction evenness and complementary specialization) and pairwise interactions of a bird-seed dispersal network of Brazilian Atlantic Forest. As result, both processes predicted connectance and nestedness. However, nestedness was mainly influenced by neutral processes. The temporal overlap between plants with ripe fruits and the presence of birds, as a process related to the niche, was the most parsimonious model able of predicting the pairwise interactions. Besides the conserved structural properties of mutualistic networks, studies also have showed that different species may play different roles in the networks. Among them, the centrality of species is one of the most important since central species are responsible for maintaining the structure, stability and biodiversity in ecological networks. However, the relevance of central species for the maintenance of the functional diversity in ecological networks remains unknown. Thus, the second chapter of this thesis introduced the concept of functional diversity of partners in ecological networks. We analysed the relationship between the functional diversity of partners and the centrality of fruit-eating birds in a seed dispersal network of the Brazilian Atlantic Forest. Given the importance of central species in ecological networks, we also evaluated the mechanisms underlying the centrality of the fruit-eating birds. We found strong correlation between the functional diversity of partners and the centrality of fruit-eating birds independent of the phylogenetic relatedness of species. In relation to the mechanism underlying the centrality of birds, species abundance had the strongest power of explanation, followed by the level of frugivory and ground-foraging. Therefore, besides central species being important to the structure, stability and biodiversity of ecological networks, this chapter shows that central fruit-eating birds are also important for the maintenance of functional diversity of bird-dispersed plants in seed dispersal networks. In conclusion, the results of this thesis enhance the importance of neutral-based processes to predict the structure and pairwise interactions in seed dispersal networks, as well as underlying the centrality of fruit-eating birds, which is positively related to the functional diversity of plants with which they interact.

Keywords: Atlantic Forest, abundance, centrality, functional diversity, functional traits, frugivory, mutualistic networks, neutral-based process, network structure, niche-based process

SUMÁRIO

1 INTRODUÇÃO GERAL

A dispersão de sementes por aves desempenha um papel fundamental na manutenção e funcionamento de ecossistemas. Esta importância é ainda mais acentuada em ecossistemas tropicais como a Mata Atlântica, onde aproximadamente 90% das espécies de plantas dependem das aves para dispersarem suas sementes (ALMEIDA-NETO *et al.*, 2008) e 25% das espécies de aves incluem frutos na sua dieta (PIZO; GALETTI, 2010). As interações entre aves dispersoras de sementes e plantas ornitocóricas (dispersadas por aves) constituem um tipo de interação mutualística, onde a ave se beneficia dos frutos das plantas como item alimentar e a planta se beneficia por ter suas sementes dispersas pelas aves (JORDANO, 1987).

Em escala de comunidades, as interações mutualísticas entre as espécies de aves e plantas podem ser representadas por ligações ou conexões gerando uma rede de interações entre as espécies (JORDANO; BASCOMPTE; OLESEN, 2003) a qual é chamada neste estudo de rede de dispersão de sementes. Assim, o estudo destas redes de interações mutualísticas permite avaliar diversas características das redes como um todo e também das interações entre os pares de espécies e o respectivo papel de cada espécie na rede (e.g. BASCOMPTE *et al.*, 2003; BASCOMPTE; JORDANO, 2007; JORDANO; BASCOMPTE; OLESEN, 2003; VAZQUEZ *et al.*, 2009).

A partir dos avanços nas análises de redes de interação mutualísticas em escala de comunidades, diversos estudos demostraram que redes mutualísticas exibem propriedades estruturais semelhantes (BASCOMPTE; JORDANO, 2007; JORDANO, 1987; VAZQUEZ *et al.*, 2009). As semelhanças estão vinculadas à parâmetros estruturais como a organização aninhada da matriz de interação, onde as espécies com muitas interações interagem entre si e com as espécies com poucas interações (BASCOMPTE *et al.*, 2003). Outros padrões estruturais m redes mutualísticas são baixa proporção de interações observadas frente às possíveis considerando todas as espécies interagindo (i.e. baixa conectância) (JORDANO, 1987; OLESEN, JENS M.; JORDANO, 2002), presença de módulos (OLESEN, JENS M *et al.*, 2007) e a distribuição assimétrica das ligações, onde muitas espécies interagem com número restrito de parceiros e poucas espécies interagem com muitas espécies de parceiros (JORDANO; BASCOMPTE; OLESEN, 2003).

Duas hipóteses centrais têm sido propostas para explicar estes padrões estruturais encontrados em redes mutualísticas e as interações entre os pares de espécies: i) a hipótese da neutralidade assume que os padrões topológicos das redes e suas interações são resultados da interação aleatória dos indivíduos. Desta forma, as espécies mais abundantes interagem com maior frequência e principalmente com espécies também mais abundantes (DUPONT; HANSEN; OLESEN, 2003; VÁZQUEZ *et al.*, 2007); e ii) a hipótese das ligações proibidas assume que processos relacionados ao nicho restringem as interações. Assim, as interações são impostas pela complementaridade das espécies em relação a traços fenotípicos, sobreposição espacial e temporal (BASCOMPTE; JORDANO, 2007; JORDANO; BASCOMPTE; OLESEN, 2003; OLESEN, J. M. *et al.*, 2010; SANTAMARÍA; RODRÍGUEZ-GIRONÉS, 2007; STANG; KLINKHAMER; MEIJDEN, 2007).

A partir da hipótese das ligações proibidas, a interação só ocorre entre espécies que apresentam complementaridade morfológica, espacial e fenológica, independente das suas abundâncias. Por outro lado, duas espécies não podem interagir se não são complementares quanto à morfologia (barreira morfológica) e se não coocorrem no tempo e espaço, independente das suas abundâncias (BASCOMPTE; JORDANO, 2007; JORDANO; BASCOMPTE; OLESEN, 2003; OLESEN, J. M. *et al.*, 2010). Apesar de postas como duas hipóteses distintas, tem sido demonstrado que processos estocásticos, relacionados à abundancia, e determinísticos, relacionado ao nicho, podem conjuntamente influenciar na determinação da estrutura de redes mutualísticas (e.g. BASCOMPTE; JORDANO, 2007; VÁZQUEZ; CHACOFF; CAGNOLO, 2009).

Recentemente, alguns estudos vêm buscando compreender melhor a importância relativa destes processos, principalmente para redes de polinização (e.g. VÁZQUEZ; CHACOFF; CAGNOLO, 2009; MARUYAMA *et al.*, 2014; OLITO; FOX, 2014; VIZENTIN-BUGONI; MARUYAMA; SAZIMA, 2014). No entanto, pouco sabemos sobre estes padrões em redes de dispersão de sementes, principalmente considerando uma análise integrada de processos neutros e relacionados ao nicho (e.g. GONZÁLEZ-CASTRO *et al.*, 2015; OLESEN, J. M. *et al.*, 2010). Assim, o **Capítulo 1** desta tese busca avaliar, a partir de modelos probabilísticos, a influência de processos neutros (abundância relativa e produtividade de frutos) ou relacionados ao nicho (barreira morfológica, sobreposição espacial e temporal de ocorrência) na topologia e determinação da

frequência das interações par a par de uma rede mutualística de dispersão de sementes por aves da Mata Atlântica.

O estudo das interações das espécies por intermédio da análise de redes também permite avaliar o papel das espécies no contexto da rede com um todo (e.g. OLESEN, JENS M *et al.*, 2007; PALACIO; VALDERRAMA-ARDILA; KATTAN, 2016; SEBASTIÁN-GONZÁLEZ, 2017). Tendo em vista a manutenção da estrutura, dinâmica e estabilidade das redes, a centralidade das espécies na rede é tida como uma das propriedades mais importantes (FREEMAN, 1979). A centralidade das espécies pode ser medida pela simples riqueza de parceiros (i.e., espécies com as quais interage) ou por sua posição na estrutura da rede, com base em suas interações (NOOY; MRVAR; BATAGELJ, 2005). Neste caso, os dispersores de sementes podem atuar como centrais por compartilharem muitos recursos com outras espécies de dispersores (centralidade por proximidade) ou por atuarem como conectores, compartilhando recursos com espécies que não possuem um recurso em comum (FREEMAN, 1979; MELLO *et al.*, 2015).

Por consumirem frutos de muitas espécies de plantas e/ou compartilharem distintas espécies de plantas com outras aves, espécies centrais de aves podem apresentar também um papel importante na manutenção da diversidade funcional de plantas na rede de interação. Este papel funcional das aves centrais dependerá das características das espécies de plantas com as quais elas interagem (e.g. tamanho da semente, altura da planta, forma de vida, etc.). No entanto, pouco sabemos sobre o papel funcional das espécies centrais dentro do contexto de redes de interação.

Desta forma, no **Capítulo 2** desta tese apresenta pela primeira vez o conceito de diversidade funcional de parceiros e avalia a relação deste papel funcional das espécies de aves com suas respectivas centralidades. Assim, pudemos avaliar se espécies de aves importantes na manutenção da estrutura das redes também apresentam um papel relevante na manutenção da diversidade funcional de plantas ornitocóricas na rede. Dada a importância das espécies centrais, neste capítulo também foi avaliado quais as variáveis determinantes da centralidade das aves de uma rede de dispersão de sementes da Mata Atlântica.

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3 CAPÍTULO 1

DETERMINANTES LOCAIS DA ESTRUTURA DE UMA REDE TROPICAL DE DISPERSÃO DE SEMENTES POR AVES

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Local drivers of the structure of a tropical bird-seed dispersal network

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This is the first study evaluating the processes driving the structure and pairwise interactions of a Neotropical bird-seed dispersal network.

Abstract

One of the major challenges in ecology is to understand the relative importance of neutral and niche-based processes structuring species interactions within communities. The concept of neutral-based processes posits that network structure is a result of interactions between species based on their abundance. On the other hand, niche-based processes presume that network structure is shaped by constraints to interactions. Here, we evaluated the relative importance of neutral-based process, represented by species' abundance (A) and fruit production (F) models, and niche-based process, represented by spatial overlap (S), temporal overlap (T) and morphological barrier (M) models, in shaping the structure of a bird-seed dispersal network from the Brazilian Atlantic Forest. We evaluated the ability of each model, singly or in combination, to predict the general structure (represented by connectance, nestedness (*NODF*), weight nestedness (*WNODF*), interaction evenness and complementary specialization) and microstructure of the network (i.e. the frequency of pairwise interactions). Only nestedness (both *NODF* and *WNODF*) was predicted by at least one model. *NODF* and *WNODF* were predicted by a neutral-based process (A), by a combination of niche-based processes (ST and STM) and by both neutral- and niche-based processes (AM). *NODF* was also predicted by F and FM model. Regarding microstructure, temporal overlap (T) was the most parsimonious model able to predict it. Our findings reveal that a combination of neutral and niche-based processes are good predictors of the general structure (*NODF* and *WNODF*) of the bird-seed dispersal network and a niche-based process is the best predictor of the network's microstructure.

Keywords Atlantic Forest; forbidden links; frugivory; mutualistic network, neutrality

Introduction

One of the major challenges in ecology is to understand the relative importance of neutral and niche-based processes in structuring species interactions within communities (e.g. Vázquez et al. 2009). Several studies have shown that mutualistic interactions at the community-level, like pollination, seed dispersal and ant-plant networks have common structural properties (e.g. Jordano 1987; Guimarães et al. 2006; Bascompte and Jordano 2007; Bascompte and Jordano 2014). Usually, mutualistic networks exhibit an asymmetrical distribution of interactions (many species interact with a restricted number of species, while few species interact with many species) (Jordano et al. 2003). Mutualistic networks also exhibit low connectance (a small fraction of all possible interactions are actually observed) and a nested structure (specialists tend to interact with a subset of resources explored by more generalist species; Bascompte et al. 2003). Fueled in part by the discovery of these patterns, there is an ongoing debate concerning the underlying mechanism that determine these conserved structural properties of mutualistic networks.

Neutral and niche-based processes have been considered as two of the main drivers of the structure of mutualistic networks. Two broad drivers have been considered as responsible for the structure of mutualistic networks. On the one hand, the concept of neutral-based processes (also called neutrality hypothesis or abundance hypothesis) presumes that network structure is the result of random interactions between individuals based on their abundance (Dupont et al. 2003; Vázquez et al. 2007; Krishna et al. 2008). Thereby, the more abundant species will interact more frequently and with more species than rarer species. On the other hand, there is the concept of niche-based processes, referred to in the network literature as the "forbidden links" hypothesis (Jordano et al. 2003) or "biological constraints" hypothesis (e.g. Olito and Fox 2014; Gonzalez and

Loiselle 2016) or "phenotypic traits" hypothesis (e.g. González-Castro et al. 2015). This concept of niche-based processes presumes that interactions are shaped by constraints to interactions imposed by the lack of complementarity in spatial and temporal distributions and morphological mismatches between the species involved (e.g. Jordano et al. 2003; Bascompte and Jordano 2007; Santamaría and Rodríguez-Gironés 2007; Stang et al. 2007; Olesen et al. 2010). Forbidden links thus arise when two species do not interact due to a lack of spatio-temporal co-occurrence or morphological constraints, irrespective of their abundance (Jordano et al. 2003; Bascompte and Jordano 2007; Olesen et al. 2010). Conversely, species with high spatial and/or temporal co-occurrence tend to present high probability of interaction, which results in higher chances to observe the interactions. The current consensus is that a combination of neutral- and niche-based processes are responsible for the observed network structure (e.g. Bascompte and Jordano 2007; Vázquez et al. 2009). However, there is much variation in their relative importance depending on the system being considered (Burns 2006; Vázquez et al. 2009; Olito and Fox 2014; Maruyama et al. 2014; Vizentin-Bugoni et al. 2014; González-Castro et al. 2015). Finally, a recent literature review suggests a "neutral–niche *continuum* model" where the relative importance of these contrasting processes depends on the amount of functional diversity in the system (Vizentin-Bugoni et al. 2018).

The first studies that aimed to understand the processes and mechanisms behind recurrent structural properties evaluated how neutral- and /or niched-based process were able to predict general network structure (Santamaría and Rodríguez-Gironés 2007; Stang et al. 2007; Vázquez et al. 2007; Encinas-Viso et al. 2012). In the last decade, this debate has gone beyond explaining general network structure and begun to evaluate the degree to which these processes explain network microstructure, that is, the frequency of individual pairwise interactions between species (Burns 2006; Junker et al. 2010; Kaiser-

Bunbury et al. 2014; Sazatornil et al. 2016). Recently, some studies used a methodological framework proposed by Vázquez et al. (2009) to evaluate the relative importance of neutral-based and niche-based processes on both general network structure and microstructure. Most of the mutualistic networks addressed by these studies were insect-plant (e.g. Vázquez et al. 2009; Olito and Fox 2014) and hummingbird-plant pollination networks (e.g. Maruyama et al. 2014; Vizentin-Bugoni et al. 2014; Gonzalez and Loiselle 2016). However, the processes underlying the general network structure and microstructure of bird-seed dispersal networks have been scarcely studied (Burns 2006; González-Castro et al. 2015). Seed dispersal has been recognized as a key ecological function worldwide (Jordano et al. 2011). The importance of seed dispersal interactions is accentuated in Neotropical forests, where about 25 to 30% of birds include fruits in their diet (Pizo and Galetti 2010). Particularly in ecosystems like the Brazilian Atlantic Forest, about 45 to 90% of tree species are dependent on seed dispersal by vertebrates and almost 40% of these tree species are dispersed exclusively by birds (Almeida-Neto et al. 2008a). Therefore, understanding which factors determine bird-plant interaction patterns plays a central role in the forest's maintenance and conservation of seed dispersal, a key ecological function in Neotropical forests. Nevertheless, an integrated analysis of the roles of neutral and niche-based processes on the patterns of Neotropical mega-diverse bird-seed dispersal networks is still missing.

Here, we evaluated the combined ability of neutral- and niche-based processes to predict the general structure and the microstructure of a bird-seed dispersal network in the Brazilian Atlantic Forest. Taking into account the "neutral–niche *continuum* model", niche-based processes are expected to be dominant drivers of interactions in communities with high functional diversity, such as in highly diverse tropical areas (Vizentin-Bugoni et al. 2018). Given the positive relationship between species richness and functional

diversity (Petchey and Gaston 2002), it is expected that the plant and bird assemblages of the mega-diverse Brazilian Atlantic Forest also present high functional diversity. Therefore, we expected that, in general, niche-based process will be stronger predictors of the general structure and microstructure of the bird-seed dispersal network evaluated.

Material and Methods

Study area and sampling design

We carried out the study in the northern coast of Paraná, Brazil (Atlantic Forest *sensu stricto*, 25º 10´ - 25º 14´ S and 48º 17´ - 48º 27´ W), at the protected areas Reserva Natural Papagaio-de-cara-roxa and Reserva Natural Salto Morato. The regional climate is humid subtropical, with a regional average annual temperature between 19ºC and 21ºC and an average annual precipitation of 2403 mm (Vanhoni and Mendonça 2008).

We conducted the interaction observations during field work from April 2011 to October 2012 in 48 plots of 100 x 10 meters (0.1 ha) each. Plots encompassed a range of successional stages (from 18 to almost 100 years old post-disturbance forests that suffered either clear cut or selective logging) and altitudes (from 20 to 270 meters), reflecting the landscape heterogeneity of the northern coastal forests of Paraná (Kauano et al. 2012). In this way, we constructed a regional bird-seed dispersal network which includes all forest habitats available and the variation due to plot age (see Devoto et al. 2011 for a similar approach). We sampled 8 to 13 plots in a day for about 10 hours per day. We sampled each plot once a month. All bird-dispersed plant species observed were included. In each sampling, two observers registered the interactions between plants and fruit-eating birds. For each fruiting species, we observed at least three individuals twice a day, at different times of the day, for about 10 minutes, until the sum of observations amounted to about one hour per day. After 10 minutes of observation, if there were still some birds

consuming fruits, the observations continued until all bird individuals recorded during the census had left the plant. When a minimum of three individuals of a given plant species were not available, we extended observation time on the individuals already found (at different times of the day), to complete one hour of observation per day (see the Online Resource 1 of the Electronic Supplementary Material for more details about the sampling effort per plant species).

We did not consider the interactions with bird species assumed to be seed predators (e.g. Psittacidae) and those where the birds did not swallow the seeds (i.e. pulp-pecking birds). Furthermore, we did not consider interactions as dispersal when large fruits with large seeds (e.g. *Campomanesia* spp.) were eaten piecemeal by small to medium birds that clearly did not ingest the seeds. In contrast, we did consider interactions as dispersal when infructescences with small seeds (e.g. *Piper* spp. and *Cecropia* spp.) were eaten piecemeal.

Based on interaction records, we built a quantitative interaction matrix ($Y = [y_{ij}]$) between fruit-eating birds j and bird-dispersed plants i in which rows and columns corresponded to plant and bird species, respectively. We considered each visit of a given bird to consume fruits of a given plant as a unique interaction event (independent of the number of fruits consumed by birds). Therefore, the cells y_{ij} contained an integer number representing the number of visits of birds j in plant species i. We estimated sampling completeness of interactions based on the Chao1 estimator of interaction richness following Devoto et al. (2012).

Neutral-based processes

We considered two measures of resource abundance to build neutral-based models, species and fruit abundance, because there is support that both abundance of

fruiting plants and fruit availability are important drivers of frugivore abundance (Levey 1988; Loiselle and Blake 1993; Blendinger et al. 2012) and frequency of fruit consumption (Blendinger et al. 2012). However, little is known about the relative importance of plant abundance and fruit availability in the structure of seed dispersal networks. We therefore considered these two measures as neutral-based processes: 1) For species abundance, we considered the relative abundance of plant individuals and birds, that is, the number of individuals of plant and bird species relative to the total number of individuals in the sampled community; 2) For fruit production, we considered the mean fruit production of plants (without multiplying by the abundance of the plant species) and the relative abundance of bird species. Each variable is described below.

Species abundance

We estimated the abundance of each plant species by counting the number of individuals in subplots within each of the 48 plots (100 x 10 m). Thus, we counted tree species in 48 subplots (50 x 6m), while we counted herbs, lianas, shrubs and epiphytes in 48 smaller subplots (50 x 3m). Due to the difficulty of distinguishing liana individuals, we considered each tangle of the same species of liana on the same tree as an individual.

We calculated bird species abundance from fixed radius point censuses (adapted from Bibby et al.1992) for each of 48 plots (100 x 10 m). We sampled bird abundance in six months from October 2011 to May 2012, except for January and April due to rainy weather. In each month sampled, we sampled bird abundance in eight plots each day, for six days, randomizing the order of plot sampling. Thus, we sampled each point census once per month of sampling. We remained 10 minutes in each point and recorded each bird seen or heard within a radius of 50 meters. To estimate the abundance of bird species we calculated the index of point abundance (IPA) for each species dividing the sum of

records for each species by the number of points sampled (n = 288), that is the number of points (n = 48) multiplied by the sampling months (n = 6) (Vielliard et al. 2010).

We built the abundance matrix (A) where each cell contains the probability of the interaction between the plant species *i* and the bird species *j* given by the product of plant relative abundance (a_i) and bird relative abundance (a_j) ($A = a_i a_j$). Therefore, this model assumed interactions between more abundant species are more likely to occur.

Fruit production

We estimated fruit production monthly by the number of mature fruits produced by each species, from April 2011 to March 2012. Whenever possible, we evaluated three individuals, of each species, with good visibility. We followed each plant from the beginning of fruit maturation until the end of fruit availability (Sun and Moermond 1997). We used visual counts to estimate the number of fruits in each plant (adapted from Chapman et al. 1992). When it was not possible to count all the fruits (because they were too many or difficult to see), we counted the fruits in a smaller representative area and we extrapolated to the rest of the individual. We then multiplied the number of fruits by the estimated fraction of ripe fruits on the plant in each phenology sampling (rounded to the nearest quarter decimal: 0.25, 0.50, 0.75 or 1). After this, we evaluated the total accumulated of each individual across months. Thus, we calculated the mean fruit production for each species as the sum of fruit produced by all individuals sampled from a given species divided by the number of individuals sampled. Finally, we built the fruit production matrix (F) where the probability of interaction is given by the product of relative mean fruit production of plant species *i* (f_i) (without multiplying by the abundance of the plant species) and bird relative abundances (a_j) ($F = f_i a_j$).

Niche-based processes

As niche-based processes, we considered spatial and temporal overlap, and morphological constraints among each plant and bird species in the seed dispersal network.

Spatial overlap

We assumed that spatial overlap between bird and plant species is mainly due to similar requirements of environmental niche. Therefore, we evaluated the spatial overlap as the co-occurrence of each plant and bird species in each plot, irrespective of whether plants were fruiting. Initially, we built the matrices of occurrences of plants (O^s_i) and birds (O^s_j) in plots, with species in rows and plots in columns. Then, we built the spatial overlap matrix (S) from multiplication of species occurrence matrices of plants and birds on the 48 plots ($S = O^s_i * O^s_j{}'$, where the symbol' indicates the transpose of the matrix). Thus, the value in each cell corresponds to the number of plots that a given plant species *i* co-occurred with a given bird species *j*. In other words, this model assumes that the more times a given pair of species co-occurred in plots, the more likely they were to interact. Thus, our spatial overlap model assumes no spatial segregation or limitations in dispersal ability and the species with no spatial co-occurrence had zero probability of interaction, resulting in a forbidden link.

Temporal Overlap

Conceptually, this model assumes that if a plant in the fruiting phenophase and a bird species occur anywhere in the study area at a given time, the bird should be able to access the plant resulting in an interaction between them. We thus evaluated temporal overlap by co-occurrence of each plant in fruiting phenophase and bird species in every month of a year. Initially, we built the matrices of occurrences of fruiting phenophase of plants (O^t_i) and birds (O^t_j) in every month of a year, with species in rows and months in

columns. Then, we built the temporal overlap matrix (T) from multiplication of species occurrence matrices of plants and birds on every month of a year ($T = O^t_i * O^t_j'$, where the symbol' indicates the transpose of the matrix). Thus, the value in each cell corresponds to the number of months that a given plant species *i* co-occurred with a given bird species *j*. In other words, if a given pair of species co-occurred in several months, they presented a higher probability of interaction. The species with no temporal co-occurrence resulted in a forbidden link.

Morphological barriers

Following the concept of exploitation barrier on Santamaría and Rodríguez-Gironés (2007), we considered it a morphological barrier when an interaction cannot occur due to the morphological constraints between species. In bird-seed dispersal networks, the size coupling between fruit size and gape width is the most usual morphological constraint (Wheelwright 1985; Burns 2013). Gape width, i.e. the external distance between commissural points, was measured from birds captured in mist nets during field work. For the species that were not captured in mist nets, we measured gape width from specimens from the Museu de História Natural Capão da Imbuia or obtained them from literature (for references see the Database in Electronic Supplementary Material).

Eklöf et al. (2013) also suggested that fruit size and gape width are the most successful combinations to explain whether two species interact. Unfortunately, the effect of seed width is usually missing, so we considered seed width and fruit width of plants as morphological barriers in relation to the gape width of birds.To estimate mean seed and fruit width we collected data on three individuals of each species, whenever possible, and we measured 10 fruits and 10 seeds of each individual. When we could not find three

individuals, we collected more fruits from each individual found to sum up 30 fruits and seeds. We measured fruit and seed width with the *software* Image J from images of seeds displayed on graph paper with millimetric scale.

Then, we built a morphological barrier matrix (M) with seed width on the rows and gape width on the columns (seed width approach). We considered it a morphological match when seed width of plant *i* was smaller than gape width of bird *j*, the interactions was thus possible and we assigned the cell a value of one. On the other hand, we considered it a morphological barrier when the seed width of plant *i* was equal or larger than the gape width of bird *j*, constituting a forbidden link. In this case, we assigned a zero value to the cell. We also built a morphological barrier matrix considering the fruit width as a constraint factor in relation to the gape width of birds (fruit width approach). We did this in the same way that we constructed the morphological barrier matrix by the seed width approach.

However, we made several observations in the field of birds handling fruits in which we detected that birds can swallow fruits larger than their gape width. In addition, masher birds can crush fruits in their bills, then large berries with smaller seeds that could not be easily separated from pulp were usually swallowed (Moermond and Denslow 1985), which generated a valid interaction. From this, before we started the analyses, we decide initially to evaluate which trait, seed or fruit width, is a real constraint factor in relation to the gape width of birds. To this end, we calculated how many links were considered as forbidden links when we used each trait by a binary network considering zero for forbidden links and one for possible links. Then, we compared these matrices with the observed matrix (Y) and calculated how many links considered as forbidden links in each approach were actually observed in field work (i.e. false forbidden links). We found that if fruit width trait was considered, 22% (n = 1364) of total possible links

(L = 6120) were considered as forbidden links, among them 39 (2.9%) were observed interactions in field work. On the other hand, when seed width trait was considered, 10% (n = 585) of total possible links (L = 6120) were considered as forbidden links, among them 9 (1.5%) were observed interactions in field work. In other words, when considering fruit width there were more forbidden links (i.e. more restrictive) than when considering seed width, but the chance to include a realized interactions as a forbidden link (false forbidden links) is greater. Thus, we decided to use seed width since is more conservative and seems to be a biologically meaningful measure to use as a morphological barrier in our seed dispersal network.

Predictive models

To evaluate the local drivers structuring the seed dispersal network, we rescaled all the matrices above (A, F, S, T, and M) dividing each cell by the matrix sum, in a manner that elements added up to one. Therefore, we transformed all the matrices in interaction probability models (following Vázquez et al. 2009). Then, we calculated the combined probabilities as the element-wise multiplication of matrices A, F, S, T, and M, again rescaling the resulting matrices so that their elements added up to one (Vázquez et al. 2009). Before proceeding with analyses, we tested the correlation among the probability models in order to avoid the multiplication of non-independent models. Given the strong correlation found between the models considering the abundance of species (A) and the spatial overlap (S) (r Mantel = 58%; p = 0.001; Online Resource 2, Electronic Supplementary Material), we excluded the models that involve the multiplication of these non-independent matrices (A and S) from the model comparison. We thus generated 23 probability matrices from combinations of relative abundance, fruit production, temporal and spatial overlap and morphological barrier (A, F, S, T, M, AF, AT, AM, FS, FT, FM, ST, SM, TM, AFM, AFT, ATM, FST, FSM, FTM, STM, AFTM and FSTM). These

combined matrices represent the expected probability under the joint influence of the factors considered (Vázquez et al. 2009). For example, each cell in FSM model represents the probability of occurrence of a certain plant-bird interaction which results from jointly considering the fruit production (F), spatial-overlap (S) and morphological barrier (M) of the pair of species involved. Accordingly, the implicit hypothesis in each model is that the factors considered (e.g. FSM) are able to explain a significant portion of the observed structure of the network. In addition, we built a benchmark null model (Null) for comparison with the other 23 probability matrices, which considers that all pairwise interactions had the same probability $1/i*j$ of occurrence, where i and j are the numbers of plant and animal species in the network (see Vázquez et al. 2009 for a similar approach).

Analysis of general network structure

Since we intended to evaluate which of our models were able to predict general network structure, we summarized the network's structure using structural properties notably conserved in seed dispersal networks (connectance and nestedness) and frequently used network metrics (interaction evenness and complementary specialization) (Vázquez et al. 2009; Vizentin-Bugoni et al. 2014; Olito and Fox 2014). Connectance (C) is the proportion of total possible links in the network that were actually observed. This metric varies from 0 to 1, where 1 indicates that 100% of possible interactions were observed, that means, all fruit-eating birds interacted with all plant species. Nestedness describes the degree to which specialists interact with proper subsets of the species that generalists interact with, and was calculated using the *NODF* (Nestedness metric based on overlap and decreasing fill, Almeida-Neto et al. 2008b) and *WNODF* (Weighted nestedness metric based on overlap and decreasing fill, Almeida-Neto and Ulrich 2011). Both metrics of nestedness vary between 0 and 100, with 100 indicating perfect nestedness. While

NODF uses qualitative data (presence/absence) of interactions, *WNODF* is a quantitative index for nestedness, weighting the nestedness contribution of different observations according to their frequencies. Interaction evenness (*IE*), similarly to Shannon's index, describe the variation on interaction frequencies distribution between different species pairs (Tylianakis et al. 2007). Complementary specialization (H'_2) quantifies the degree of specialization of the entire network, measuring the extent to which observed interactions deviate from those that would be expected given the species marginal totals, and ranges between 0 (no selectivity) and 1 (complete selectivity) (Blüthgen et al. 2006).

We performed all analyses using R statistical software (R Core Team 2017). To evaluate the ability of our models to predict the general structure of the network, we used the 'netstat' function in 'ecolnet' package version 1.0 (Vázquez 2013). This function generates randomized networks from an observed matrix and uses the 'mgen' function to randomize probability matrices. Although the function 'mgen' does not constrain row and column totals, neither connectance, this function constrains the total number of interactions according to the observed network and is a more flexible way of conducting randomizations than other null models. For example, it allows any type of probability matrix to be used for constructing the simulated matrices. For each predictive model, we ran 1000 iterations to generate a frequency distribution and obtain a mean and 95% confidence intervals for each network metric considered above. We then compared the observed network metrics values calculated from the observed network (Y) to the network metrics values obtained from the 23 predictive models and the null model.

Analysis of microstructure

To evaluate the ability of our models to predict interaction frequencies (Y) we used a likelihood approach. We considered that in each predictive model (X) the cells *xij* are the

probabilities of occurrence for each pairwise interaction. Therefore, if a predictive model can predict the observed interactions, the cells with higher probability in X must show higher number of interactions in the observed matrix (Y). As in similar studies (e.g. Vázquez et al. 2009; Vizentin-Bugoni et al. 2014), we did this evaluation calculating the likelihood of predictive models X given the observed data (Y), and we assumed that the pairwise probability of interaction between a given plant and a given bird followed a multinomial distribution (see the formula below). Thus, the likelihood (L) of probability matrix *l* given the data is

$$L_l = \frac{F!}{\prod_{i=1}^{I}\prod_{j=1}^{J} y_{i,j}!} \prod_{i=1}^{I}\prod_{j=1}^{J} x_{ijl}^{y_{ij}}$$

where *F* is the total number of observed interactions (i.e., the sum of the elements of matrix Y), and *I* and *J* are the total number of animals and plants in Y, respectively (Vázquez et al. 2009). As mentioned above, entries *xij* are the probabilities of occurrence for each pairwise interaction in the predictive models.

We then calculated the Akaike's Information Criterion (AIC) to evaluate the predictive ability of each of our 23 models and the null model. We considered AIC = -2 ln(L) + 2k, where *k* is the number of species of each given predictive model (Vizentin-Bugoni et al. 2014). Therefore, in a model built from only one matrix (e.g. A, F, S, T or M), there were 90 plant species and 68 bird species and thus we had *k* =90 + 68 = 158. For a model built from two matrices, we had *k* = 158+ 158 = 316, and so on. Considering that the null model is simpler than any other model and that it was not properly based on a matrix, we assumed the null model had one parameter (*k* = 1), as in previous studies (Maruyama et al. 2014; Vizentin-Bugoni et al. 2014). Finally, after we calculated the

Akaike's Information Criterion (AIC) for each of the 24 models, we subtracted each model AIC from the best-fitted AIC model (i.e. the lowest AIC) to have ΔAIC value for each model.

To evaluate the ability of our models to predict network microstructure by multinomial likelihood and AIC, we used the "mlik" function on "ecolnet*"* package (Vázquez 2013).

Results

Seed dispersal network

Our seed dispersal network was composed by 90 plant species and 68 bird species (Fig. 1) and a network size of 6120 possible interactions. We recorded 496 pairwise interactions, 910 visits by birds and 6215 fruits consumed. The observed values of the general structure evaluated were C = 0.08 (Null model = 0.138 ± 0.002), $NODF$ = 13.57 (Null model = 4.27 ± 0.7), $WNODF$ = 11 (Null model = 0.949 ± 0.245), IE = 0.68 (Null model = 0.77 ± 0.003) and H'_2 = 0.24 (Null model = 0.043 = ± 0.01). Analysis of sampling completeness estimates that we recorded 53% of the links in the community (Online Resource 3).

Plant species belonged to 35 families and Melastomataceae presented the highest richness (S = 15), followed by Rubiaceae (S = 11) and Myrtaceae (S = 7). The plant species with the highest fruit consumption were *Miconia cinerascens* (n = 719), *Myrcia* cf. *glabra* (n = 644) and *Casearia sylvestris* (n = 637) representing 32% of the total fruit consumption (Fig. 1). *Miconia cinerascens* was also the species with the highest fruit production (17%), relative abundance (6%) and richness of mutualistic partners (S = 25), followed by *Casearia sylvestris* and *Hyeronima alchorneoides* (for both, S = 22). The number of plots in which plant species occurred ranged from 1 to 15 plots (Online

Resource 4). The temporal distribution of ripe fruits ranged from 1 to 7 months (Online Resource 5; for plant phenology see Online Resource 6) and the seed width ranged from 0.23 mm to 17.06 mm. (Online Resource 7).

Among birds, *Turdus albicollis* was the species that consumed the highest number of fruits (n = 830; Degree = 35), followed by *Tangara cyanocephala* (n = 488; Degree = 31) and *Tangara seledon* (n = 385; Degree = 24). The fruits consumed by these three species corresponded to 27% of all fruits consumed (Fig. 1). *Turdus albicollis* was also the species with the highest relative abundance (14%). *Chiroxiphia caudata* and *Turdus flavipes* presented the highest richness of mutualistic partners (for both, S = 35), followed by *Tangara cyanocephala* (S = 31). The number of plots in which bird species occurred ranged from 1 to 44 plots (Online Resource 4). The temporal distribution of birds' occurrences ranged from 1 to 12 months (Online Resource 5; for bird phenology see Online Resource 8) and the gape width of birds ranged from 5.7 mm in *Coereba flaveola* to 31.1 mm in *Ramphastos vitellinus* (Online Resource 7; Database).

General network structure

The models considering species abundances (A), spatio-temporal overlap (ST), and its association with morphological barrier model (AM and STM) predicted both observed nestedness (*NODF*) and weighted nestedness (*WNODF*) (Fig. 2b). Additionally, fruit production model (F) alone, as well as associated with morphological barrier model (FM) also predicted nestedness (*NODF*). For all these cases, the presence of morphological barrier (M) did not change substantially the mean predicted value of nestedness and confidence interval of the models. Despite that, no model predicted connectance accurately, FS produced values close to the observed (Fig. 2a). For interaction evenness, some models showed values closer to the observed ones (Fig. 2d) while, for

complementary specialization, all models showed lower values than the observed network.

Evaluating the contribution of each factor separately (A, F, S, T or M), the observed values of all network properties were best predicted by neutral models (A and F) in comparison to the niched-based models (S, T and M). In other words, the single models composed by neutral factors, presented network properties closer to the values of observed network than niche-based models alone.

Microstructure

The temporal overlap model (T) was the one best fitting the observed microstructure (Fig. 3). However, there were pairwise interactions from T model with intermediate to high probabilities to occur that were rarely or never observed, while there were pairwise interactions with low probabilities to occur that were observed with high frequencies in the field (Online Resource 9).

Discussion

Our findings reveal that a combination of neutral and niche-based processes were good predictors of the nestedness (*NODF* and *WNODF*) of a bird-seed dispersal network. Regarding the microstructure, a single niche-based process (T) was the most parsimonious model to predict the pairwise frequencies of interaction.

General network structure

Our observed network showed a very low connectance with only 8 % of possible interactions observed ($C = 0.08$), which is common in species-rich networks (Jordano 1987; Blüthgen et al. 2007). Nestedness was influenced mainly by neutral-based process (A), since this model alone was able to predict the observed values of nestedness. Indeed,

the literature suggests that the nested pattern of seed dispersal networks is mostly explained by relative species abundance (Krishna et al. 2008). Although the relative abundance of a species is considered as a neutral-based process, it is important to note that species abundances may be also driven by niche-based processes (Vizentin-Bugoni et al. 2014). Additionally, the model containing all niche-based processes (STM) was also able to predict *NODF* and *WNODF* of the observed network. Indeed, others studies showed that niche-based processes are also important drivers of the nestedness in mutualistic networks (Krishna et al. 2008; Olito and Fox 2014, González-Castro et al. 2015).

Our observed network showed a low but significant complementary specialization (H'_2 = 0.24) as in other seed dispersal networks (e.g. Blüthgen et al. 2007). However, the observed complementary specialization was higher than predicted by any model. This indicates that there are other niche-based processes besides spatio-temporal overlap and morphological constraints that may be increasing the observed complementary specialization, as reported for other studies (Olito and Fox 2014; Vizentin-Bugoni et al. 2014). For example, ecological and evolutionary factors like the preference by birds for one forest strata (Schleuning et al. 2011), the different levels of frugivory among bird species (Mello et al. 2015; Dalsgaard et al. 2017; Sebastián-González 2017), color preferences (Flörchinger *et al.* 2010), nutritional content (Blendinger et al. 2015; González-Castro et al. 2015; Sebastián-González 2017) or secondary metabolites (Cipollini and Levey 1997) may also constrain or favor some interactions and consequently increase network specialization.

Microstructure

We found that the temporal overlap model (T) was the most parsimonious model able to predict the pairwise interactions. Therefore a niche-based process was the dominant

driver of interactions in a highly diverse tropical area (i.e. Brazilian Atlantic Forest), as predicted by the "neutral–niche *continuum* model" (Vizentin-Bugoni et al. 2018). Temporal overlap was also an important driver of interactions in another seed dispersal network (Olesen et al. 2010), in pollination networks by insects (Vázquez et al. 2009; Olito and Fox 2015), hummingbirds (Maruyama et al. 2014; Vizentin-Bugoni et al. 2014, Gonzalez and Loiselle et al. 2016), flowerpiercers (Gonzalez and Loiselle et al. 2016) and for plant-animal mutualistic networks in general (Encinas-Viso et al. 2012).

Despite temporal overlap being the most parsimonious model able to predict the network microstructure, there were many interactions predicted by T model that were not observed (Online Resource 9). This suggests that, besides temporal overlap, other niche-based processes constrain network microstructure. On the other hand, a combination of neutral processes (i.e. species abundance) and niche-based processes were reported to be important in the establishment of pairwise bird-plant interactions in a small insular community of a Mediterranean scrubland habitat (González-Castro et al. 2015).

The importance of the temporal overlap in determining the microstructure indicates that seed dispersal networks may be strongly influenced by changes in phenology of plants and bird species, mainly migratory birds and species with seasonal altitudinal displacements. Since phenology of plant species is affected by global climate changes (e.g. Fitter and Fitter 2002; Butt et al. 2015), it is crucial that further studies includes the evaluation of the effect of phenology variations over long time spans on the interactions of plants and fruit-eating birds and their demographic outcomes (Fagan et al. 2014).

Neutral VS Niche-based processes

The spatial overlap model showed a strong correlation with the model of abundance of

species. Indeed, considering the occupancy-abundance relationship (Gaston et al. 1997; He and Gaston 2000), it is expected that species that are more abundant tend to occur in more sampling units (mainly in sampling unit with small size), justifying the correlation found. Therefore, spatial overlap includes a continuum of neutral and niche-based processes, with no clear cut separation between both processes. Additionally, despite the weak correlation between the models considering the abundance of species and temporal overlap (10%, Online Resource 2), studies suggest that both are also related because species phenologies determine the relative abundance in a specific time of the season (Encinas-Viso et al. 2012). On the other hand, the species abundance is in fact directly dependent of many niche-based processes and species interactions (e.g. competition).

Seed width versus fruit width as morphological barrier

Morphological barriers contributed little to predict the general structure and the microstructure when compared to other studies on seed dispersal networks (González-Castro et al. 2015). As there are few plant species with seed width larger than gape width, our morphological barrier matrix (M) has few forbidden links (10%, as discussed above). Thus, considering the model M, 90% of all interactions were not forbidden, while only 8% of them were realized. Consequently, the model M, alone or in combination with other models, has low power of explanation leading to its small contribution to prediction power of the general structure and microstructure.

Certainly, using fruit width instead of seed width would lead to more cases of forbidden links (22%) and the model would be more restrictive, that is, with more forbidden links. This could enhance the power of morphological barriers to predict the general structure and the microstructure, as found in others studies (e.g. Burns 2013, González-Castro et al. 2015). However, as addressed in the Methods section, we made

several observations of birds swallowing fruits larger than their gape width. Thus, in our case, the chance to determine false forbidden links (i.e. that we observed in field) is greater in the fruit width approach. Under these circumstances, the seed width approach was the more conservative and more biologically meaningful measure to use as a morphological barrier in our seed dispersal networks. Moreover, we tested and compared the microstructure predictive power of models containing morphological barrier (M) built from seed width with the models built considering fruit width. The results showed that models considering the seed width as the measure of morphological barrier were the best models among them (lower AIC values) (Online Resource 10)**.** In this way, we showed that seed width could be a better measure for morphological mismatching in studies considering forbidden links.

In conclusion, this is the first study evaluating the processes driving the structure and pairwise interactions of a Neotropical bird-seed dispersal network. While a combination of neutral and niche-based processes were good predictors of the general structure of the bird-seed dispersal network, a niche-based process (i.e. temporal overlap) best accounted for the network's microstructure. Our results thus support the expected by the "neutral–niche *continuum* model" for highly diverse tropical areas (Vizentin-Bugoni et al. 2018).

Data accessibility

We archived our raw data as Electronic Supplementary Material (Database.xlsx).

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on an earlier version of the paper.

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Fig. 1. Bird seed-dispersal network in the Atlantic Forest of Guaraqueçaba, southern Brazil. Plant species are on the left and bird species on the right. Lines represent species interactions and line thickness is proportional to the number of fruits dispersed.

Fig. 2. Observed values of general network structure (black vertical lines) and those predicted by the models (circles, mean; bar, 95% confidence interval; 1000 randomizations). The 23 probability matrices were built based on relative species abundance (A), fruit production of plants and relative abundance of birds (F), spatial overlap (S), temporal overlap (T), morphological barrier (M), and all possible combinations among these models. Null is the model in which all pairwise interactions have the same probability.

Fig. 3. Likelihood analysis considering all possible models. Lower values of ΔAIC indicate better fit of a given model in relation to the T model, which presented the best fit to the observed microstructure of network. The 23 probability matrices were built based on relative species abundance (A), fruit production of plants and relative abundance of birds (F), spatial overlap (S), temporal overlap (T), morphological barrier (M), and all possible combinations among these models. Null is the model in which all pairwise interactions have the same probability.

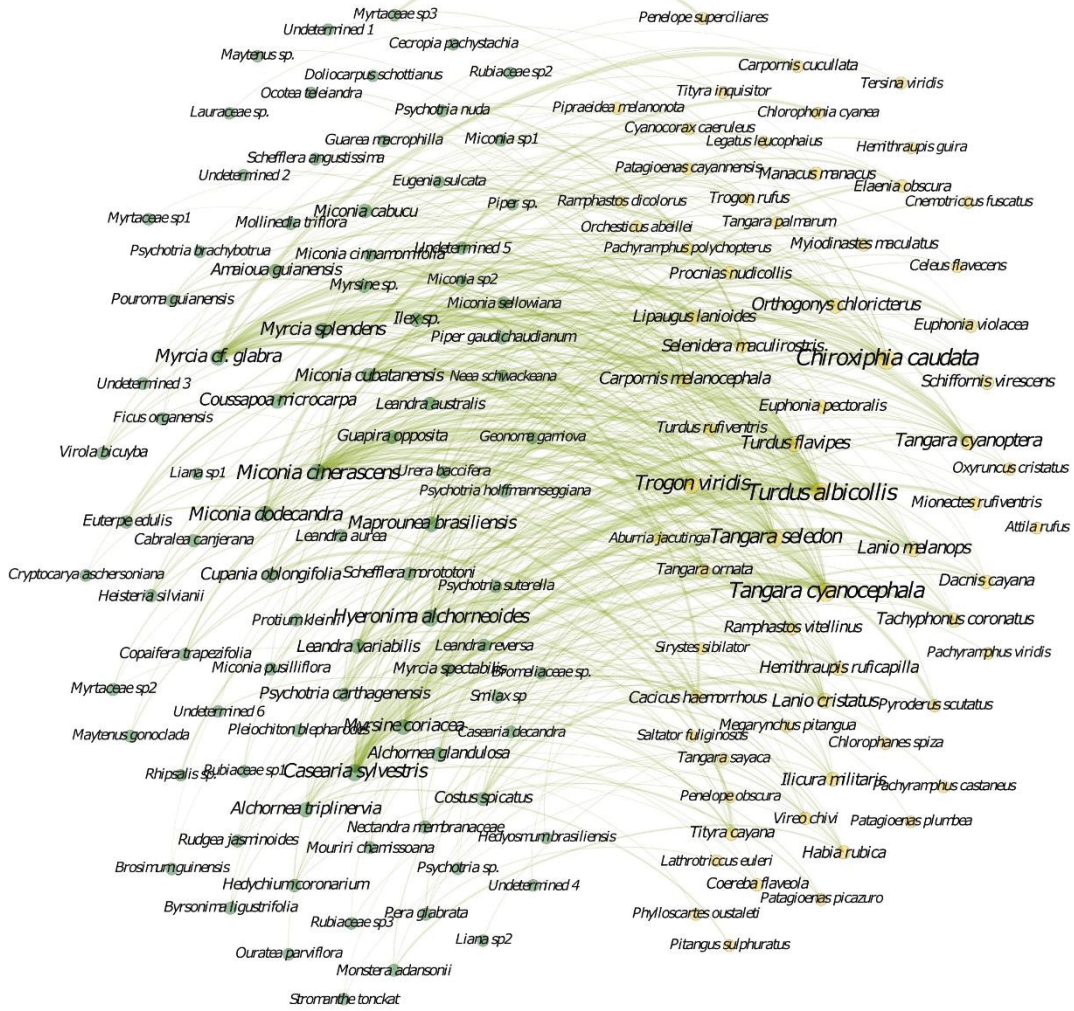
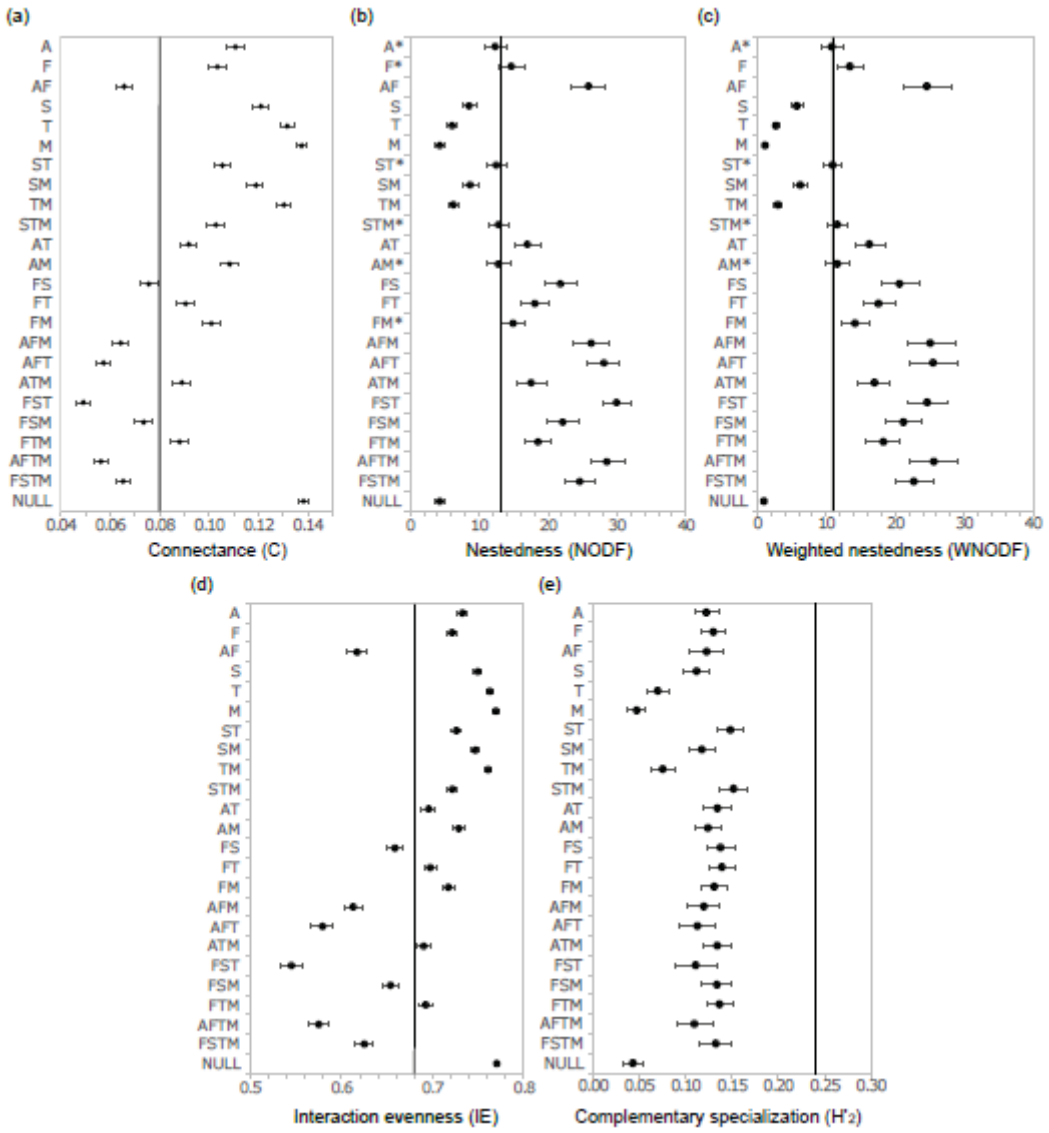

Myrtaceae sp3
Undetermined 1
Cecropia pachystachia
Maytenus sp.
Doliocarpus schottianus
Rubiaceae sp2
Ocotea teleiandra
Lauraceae sp.
Psychotria nuda
Guarea macrophilla
Miconia sp1
Schefflera angustissima
Undetermined 2
Eugenia sulcata
Myrtaceae sp1
Miconia cabucu
Piper sp.
Mollinedia triflora
Psychotria brachybotrua
Miconia cinnamomifolia
Undetermined 5
Amaioua guianensis
Myrsine sp.
Miconia sp2
Pourouma guianensis
Miconia sellowiana
Ilex sp.
Myrcia splendens
Piper gaudichaudianum
Myrcia cf. glabra
Undetermined 3
Miconia cubatanensis
Neea schwackeana
Coussapoa microcarpa
Leandra australis
Ficus organensis
Guapira opposita
Geonoma gamiova
Virola bicuyba
Liana sp1
Miconia cinerascens
Urera baccifera
Psychotria hoffmannseggiana
Euterpe edulis
Miconia dodecandra
Maprounea brasiliensis
Cabralea canjerana
Leandra aurea
Cryptocarya aschersoniana
Cupania oblongifolia
Schefflera morototoni
Psychotria suterella
Heisteria silvianii
Protium kleinii
Hyeronima alchorneoides
Leandra variabilis
Leandra reversa
Copaifera trapezifolia
Miconia pusilliflora
Myrcia spectabilis
Bromeliaceae sp.
Myrtaceae sp2
Psychotria carthagenensis
Smilax sp
Undetermined 6
Myrsine coriacea
Pleiochiton blepharodes
Casearia decandra
Maytenus gonoclada
Alchornea glandulosa
Rubiaceae sp1
Casearia sylvestris
Rhipsalis sp.
Costus spicatus
Alchornea triplinervia
Nectandra membranaceae
Rudgea jasminoides
Hedyosmum brasiliensis
Mouriri chamissoana
Brosimum guinensis
Psychotria sp.
Hedychium coronarium
Undetermined 4
Byrsonima ligustrifolia
Pera glabrata
Rubiaceae sp3
Liana sp2
Ouratea parviflora
Monstera adansonii
Stromanthe tonckat
Penelope superciliares
Carpornis cucullata
Tersina viridis
Tityra inquisitor
Pipraeidea melanonota
Chlorophonia cyanea
Cyanocorax caeruleus
Legatus leucophaius
Herpsilochmus guira
Patagioenas cayannensis
Manacus manacus
Elaenia obscura
Ramphastos dicolorus
Trogon rufus
Cnemotriccus fuscatus
Orchesticus abeillei
Tangara palmarum
Pachyramphus polychopterus
Myiodinastes maculatus
Procnias nudicollis
Celeus flavescens
Orthogonys chloricterus
Lipaugus lanioides
Euphonia violacea
Selenidera maculirostris
Chiroxiphia caudata
Carpornis melanocephala
Schiffornis virescens
Euphonia pectoralis
Turdus rufiventris
Turdus flavipes
Tangara cyanoptera
Oxyruncus cristatus
Trogon viridis
Turdus albicollis
Mionectes rufiventris
Attila rufus
Aburria jacutinga
Tangara seledon
Lanio melanops
Tangara ornata
Dacnis cayana
Tangara cyanocephala
Tachyphonus coronatus
Ramphastos vitellinus
Sirystes sibilator
Pachyramphus viridis
Herpsilochmus ruficapilla
Cacicus haemorrhous
Lanio cristatus
Pyroderus scutatus
Megarynchus pitangua
Saltator fuliginosus
Chlorophanes spiza
Tangara sayaca
Ilicura militaris
Pachyramphus castaneus
Penelope obscura
Vireo chivi
Patagioenas plumbea
Tityra cayana
Habia rubica
Lathrotriccus euleri
Coereba flaveola
Patagioenas picazuro
Phylloscartes oustaleti
Pitangus sulphuratus

Fig. 1


(a)
(b)
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FSTM
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A*
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AM*
ST*
STM*
FM*
0.04 0.06 0.08 0.10 0.12 0.14
Connectance (C)
0 10 20 30 40
Nestedness (NODF)
Weighted nestedness (WNODF)
0.5 0.6 0.7 0.8
Interaction evenness (IE)
0.00 0.05 0.10 0.15 0.20 0.25 0.30
Complementary specialization (H'2)

Fig. 2

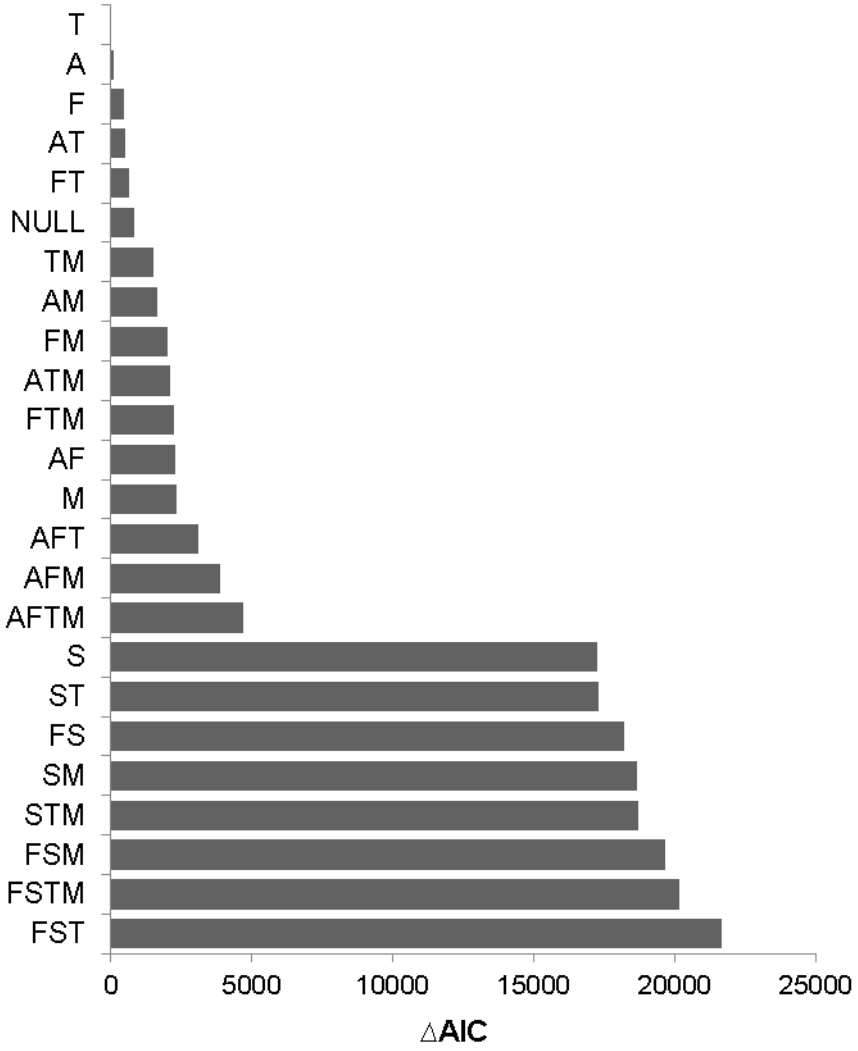
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Fig. 3

Electronic Supplementary Material

Machado-de-Souza, T., Campos, R. P., Devoto, M. and Varassin, I. G. Local drivers of the structure of a tropical bird-seed dispersal network. – **Oecologia.** E-mail: tigomachado@gmail.com

Online Resource 1

Table S1. Sampling effort per plant species.

Species	Hours	*Species*	Hours
Alchornea glandulosa	4	*Monstera adansonii*	30
Alchornea triplinervia	32	*Mouriri chamissoana*	2
Amaioua guianensis	35	*Myrcia cf. glabra*	14
Bromeliaceae sp.	1	*Myrcia spectabilis*	15
Brosimum glaucum	3	*Myrcia splendens*	14
Byrsonima ligustrifolia	4	*Myrsine coriacea*	27
Cabralea canjerana	10	*Myrsine* sp.1	15
Casearia decandra	6	*Myrtaceae* sp.1	2
Casearia sylvestris	28	*Myrtaceae* sp.2	3
Cecropia pachystachya	6	*Myrtaceae* sp.3	4
Copaifera trapezifolia	6	*Nectandra membranaceae*	6
Costus spicatus	90	*Neea pendulina*	8
Coussapoa microcarpa	30	*Ocotea teleiandra*	6
Cryptocarya aschersoniana	6	*Ouratea parviflora*	4
Cupania oblongifolia	32	*Pera glabrata*	12
Doliocarpus schottianus	8	*Piper gaudichaudianum*	24
Eugenia sulcata	2	*Piper* sp.2	3
Euterpe edulis	12	*Pleiochiton blepharodes*	2
Ficus organensis	15	*Pourouma guianensis*	4
Geonoma gamiova	24	*Protium kleinii*	14
Guapira opposita	4	*Psychotria carthagenensis*	35
Guarea macrophylla	2	*Psychotria gracilenta*	24

Species	Hours
Hedychium coronarium	8
Hedyosmum brasiliense	12
Heisteria silvianii	6
Hyeronima alchorneoides	16
Ilex sp.	9
Lauraceae sp.	1
Leandra aurea	30
Leandra australis	9
Leandra reversa	45
Leandra variabilis	84
Maprounea brasiliensis	6
Maytenus alaternoides	2
Maytenus sp.1	4
Miconia cabucu	8
Miconia cinerascens	72
Miconia cinnamomifolia	12
Miconia cubatanensis	28
Miconia dodecandra	15
Miconia pusilliflora	20
Miconia sellowiana	10
Miconia sp.1	5
Miconia sp.2	6
Mollinedia triflora	9

Species	Hours
Psychotria hoffmannseggiana	12
Psychotria nuda	84
Psychotria sp.1	3
Psychotria suterella	12
Rhipsalis sp	5
Rubiaceae sp.1	2
Rubiaceae sp.2	16
Rubiaceae sp.3	5
Rudgea jasminoides	12
Schefflera angustissima	9
Schefflera morototoni	4
Smilax sp.	4
Stromanthe tonckat	6
Undetermined 1	6
Undetermined 2	1
Undetermined 3	6
Undetermined 4	1
Undetermined 5	6
Undetermined 6	4
Undetermined 7	15
Undetermined 8	2
Urera baccifera	9
Virola bicuhyba	20

Online Resource 2

Table S2. Correlation among the probability models by Mantel test.

Models	r Mantel	P
AS	0.58	0.001*
AT	0.11	0.005*
AM	-0.04	0.762
AF	-0.01	0.596
ST	0.10	0.013*
SM	0.06	0.155
SF	-0.02	0.762
TM	0.03	0.670
TF	0.08	0.011*
MF	-0.04	0.819

*P <0.05

Online Resource 3

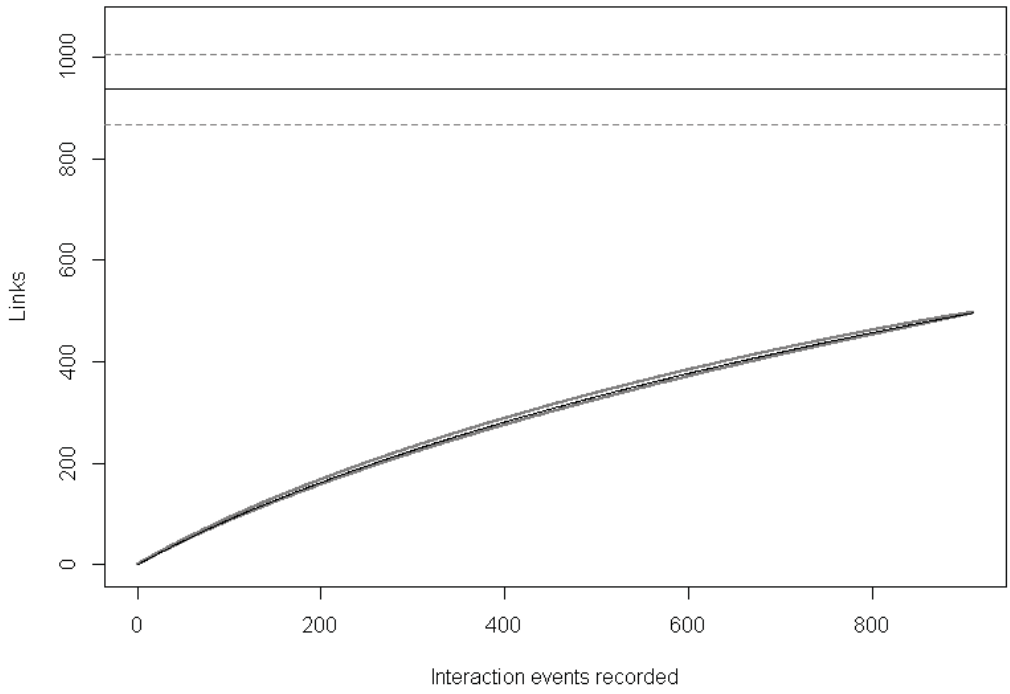


Figure S1. Sampling completeness measure from rarefaction of unique interactions and interaction events (visits) for the observed bird-seed dispersal network in the Atlantic Forest of Guaraqueçaba, southern Brazil. Horizontal black line represent the Chao 1 estimate of asymptotic species richness with 95% confidence intervals (dashed lines).

Online Resource 4

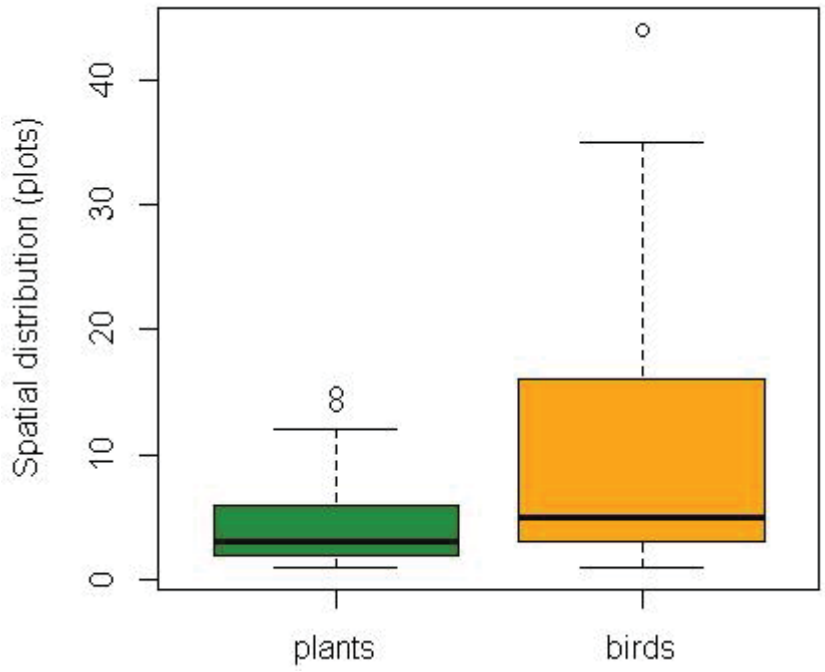


Figure S2. Boxplot evaluating the spatial distribution of species, i.e. the occurrences of plants and birds in plots.

Online Resource 5

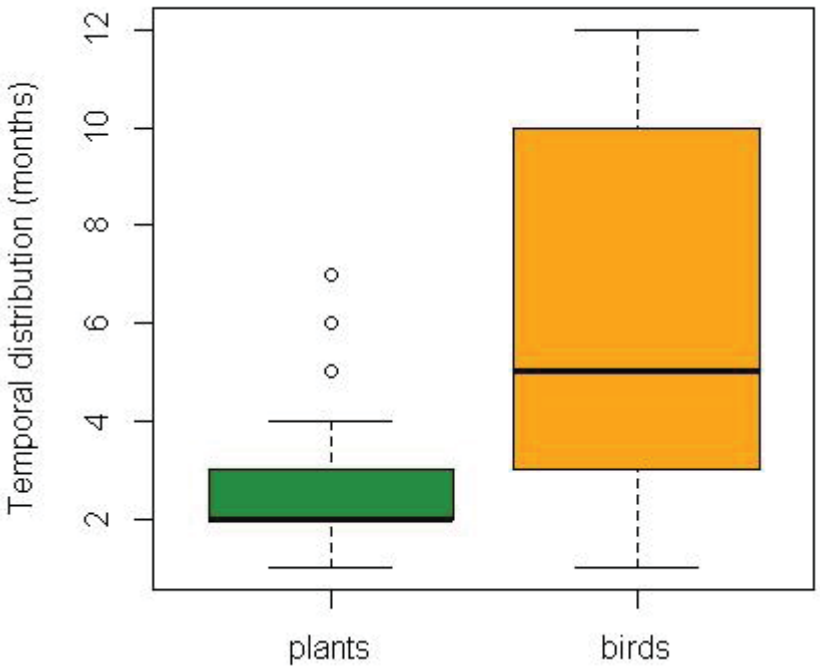


Figure S3. Boxplot evaluating the temporal distribution of species, i.e. the occurrences of plants and birds species in sampled months.

Online Resource 6

Table S3. Phenology of bird-dispersed plants in the Atlantic Forest of Guaraqueçaba, southern Brazil. The species were sorted in decreasing order of number of months fruiting. Black fills indicate the presence of a given species for a given month.

Species	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec	Total
Psychotria nuda			■	■	■	■	■	■	■				7
Costus spicatus			■	■	■	■	■	■					6
Leandra variabilis			■	■	■	■	■	■					6
Miconia cinerascens					■	■	■	■	■	■			6
Amaioua guianensis					■	■	■	■	■				5
Coussapoa microcarpa	■	■	■							■	■		5
Ficus organensis				■	■				■	■	■		5
Leandra reversa			■		■	■	■	■					5
Miconia dodecandra						■				■	■	■	5
Myrcia spectabilis						■	■	■	■	■			5
Psychotria carthagenensis						■	■	■	■	■			5
Virola bicuhyba						■	■	■	■	■			5
Alchornea triplinervia	■	■								■	■		4
Cupania oblongifolia	■									■	■	■	4
Hedyosmum brasiliense			■	■	■	■							4
Miconia cubatanensis						■	■	■	■				4
Miconia pusilliflora				■	■	■	■						4
Piper gaudichaudianum			■	■	■	■							4
Psychotria gracilenta					■	■	■	■					4
Rubiaceae sp2						■	■	■	■				4
Copaifera trapezifolia										■	■	■	3
Cryptocarya aschersoniana						■	■	■					3
Euterpe edulis					■	■		■					3
Geonoma gamiova								■	■	■			3
Heisteria silvianii	■	■										■	3
Ilex sp.			■	■	■								3
Leandra aurea				■	■	■							3
Leandra australis				■	■	■							3
Undetermined 7	■	■	■										3
Miconia cinnamomifolia			■	■	■								3
Miconia sp2								■	■	■			3
Mollinedia triflora							■	■	■				3
Monstera adansonii									■	■	■		3
Undetermined 1									■	■	■		3
Undetermined 3	■		■		■								3
Undetermined 5						■	■	■					3
Myrsine coriacea									■	■	■		3
Myrsine sp.								■	■	■			3
Myrtaceae sp2	■	■	■										3
Pera glabrata		■	■	■									3
Psychotria holffmannseggiana						■	■	■					3
Psychotria suterella							■	■	■				3
Schefflera angustissima					■	■	■						3
Urera baccifera				■	■	■							3
Byrsonima ligustrifolia				■	■								2

Species	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec	Total
Cabralea canjerana								■	■				2
Casearia decandra	■											■	2
Casearia sylvestris										■	■		2
Cecropia pachystachya						■	■						2
Doliocarpus schottianus			■	■									2
Hedychium coronarium		■	■										2
Hyeronima alchorneoides			■	■									2
Undetermined 8			■	■									2
Maprounea brasiliensis			■	■									2
Maytenus alaternoides			■	■									2
Maytenus sp.	■											■	2
Miconia cabucu											■	■	2
Miconia sellowiana							■	■					2
Undetermined 6									■	■			2
Myrcia cf. glabra				■	■								2
Myrcia splendens											■	■	2
Myrtaceae sp3									■	■			2
Nectandra membranaceae											■	■	2
Neea schwackeana										■	■		2
Ocotea teleiandra					■					■			2
Ouratea parviflora									■	■			2
Pourouma guianensis		■	■										2
Protium kleinii											■	■	2
Rubiaceae sp1					■	■							2
Rudgea jasminoides									■	■			2
Schefflera morototoni					■	■							2
Smilax sp.			■	■									2
Stromanthe tonckat									■	■			2
Alchornea glandulosa										■			1
Bromeliaceae sp.											■		1
Brosimum glaucum			■										1
Eugenia sulcata											■		1
Guapira opposita										■			1
Guarea macrophylla												■	1
Lauraceae sp.										■			1
Miconia sp1					■								1
Undetermined 2								■					1
Undetermined 4					■								1
Mouriri chamissoana					■								1
Myrtaceae sp1						■							1
Piper sp.					■								1
Pleiochiton blepharodes			■										1
Psychotria sp.					■								1
Rhipsalis sp.							■						1
Rubiaceae sp3					■								1
	9	**8**	**23**	**21**	**30**	**28**	**23**	**24**	**23**	**27**	**17**	**11**	

Online Resource 7

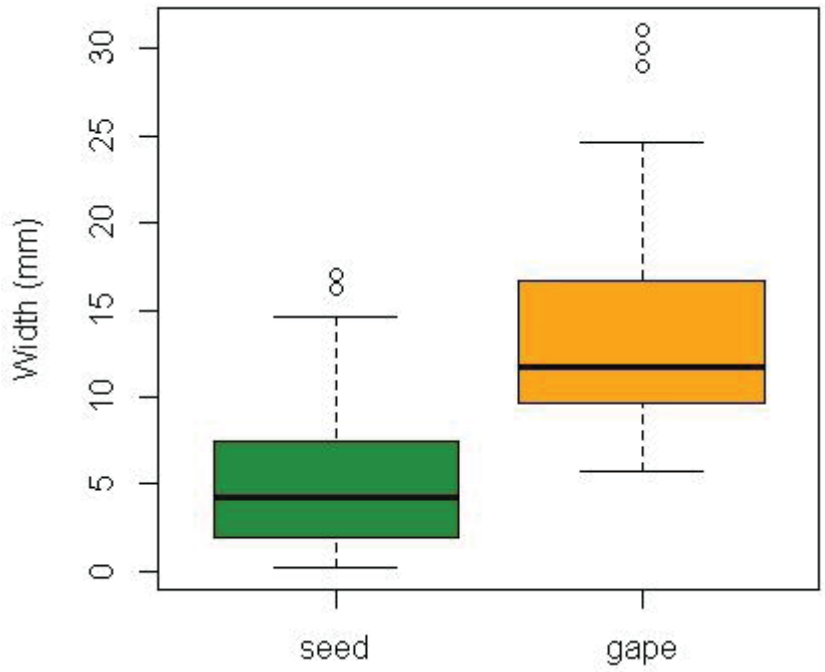


Figure S4. Boxplot evaluating seed width of plant species and gape width of birds.

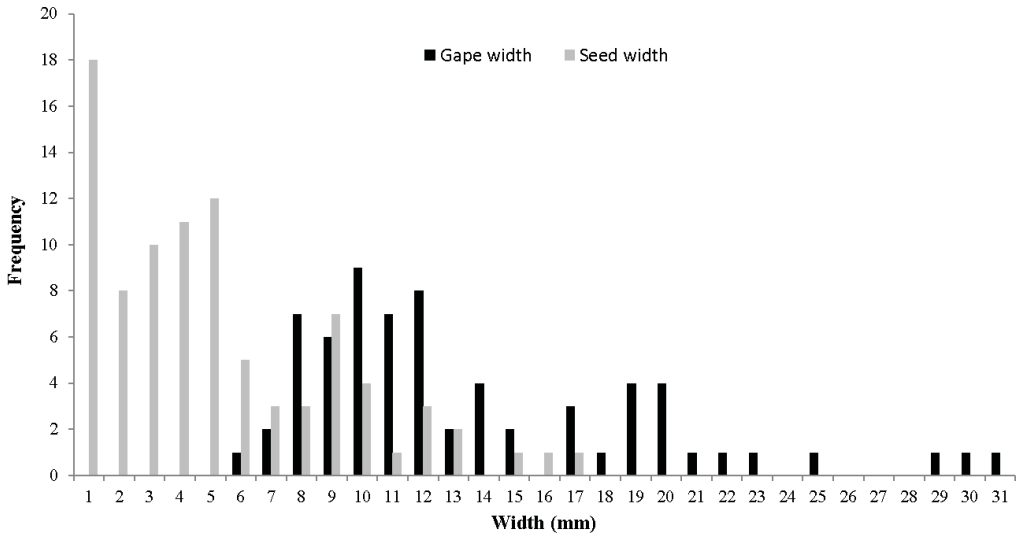


Figure S5. Species richness for each class of gape width (black bars) and seed width (gray bars) for the observed bird seed dispersal mutualistic network in the Brazilian Atlantic Forest of Guaraqueçaba, southern Brazil.

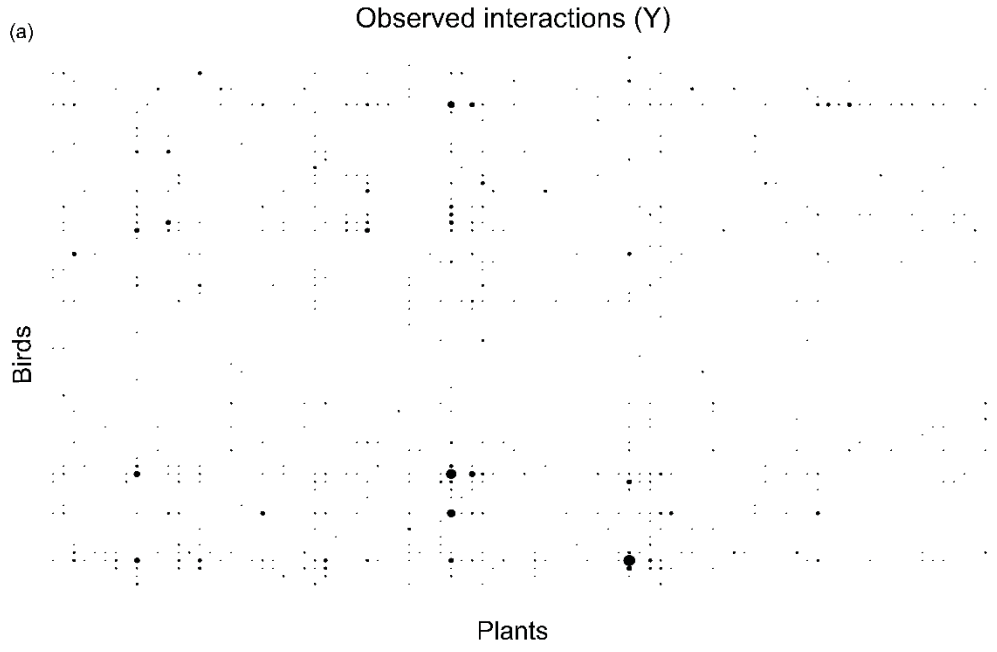
Online Resource 8

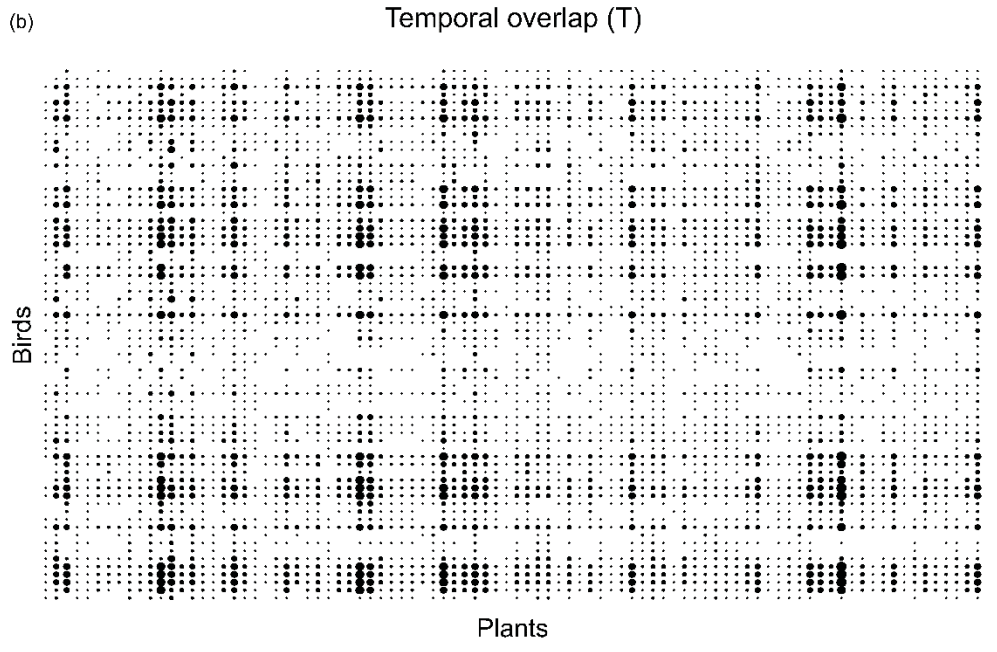
Table S4. Phenology of fruit-eating birds at the Atlantic Forest of Guaraqueçaba, southern Brazil. The species were sorted by decreasing order of number of months registered. Black fills indicate the presence of a given species for a given month.

Species	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec	Total
Chiroxiphia caudata	■	■	■	■	■	■	■	■	■	■	■	■	12
Orthogonys chloricterus	■	■	■	■	■	■	■	■	■	■	■	■	12
Schiffornis virescens	■	■	■	■	■	■	■	■	■	■	■	■	12
Tangara cyanocephala	■	■	■	■	■	■	■	■	■	■	■	■	12
Tangara cyanoptera	■	■	■	■	■	■	■	■	■	■	■	■	12
Trogon viridis	■	■	■	■	■	■	■	■	■	■	■	■	12
Turdus albicollis	■	■	■	■	■	■	■	■	■	■	■	■	12
Turdus flavipes	■	■	■	■	■	■	■	■	■	■	■	■	12
Habia rubica	■	■	■	■	■	■	■	■	■	■	■		11
Lanio melanops	■	■	■	■	■	■	■	■	■	■	■		11
Tangara seledon	■	■	■	■	■		■	■	■	■	■	■	11
Cacicus haemorrhous	■		■	■	■	■	■	■	■	■	■	■	10
Carpornis melanocephala	■	■	■			■	■	■	■	■	■	■	10
Euphonia pectoralis		■	■		■	■	■	■	■	■	■	■	10
Hemithraupis ruficapilla	■	■	■	■	■		■		■	■	■	■	10
Ilicura militaris		■	■		■	■	■	■	■	■	■	■	10
Lanio cristatus	■		■	■	■	■	■	■		■	■	■	10
Manacus manacus			■	■	■	■	■	■	■	■	■	■	10
Lipaugus lanioides			■	■	■	■	■	■	■		■	■	9
Tachyphonus coronatus	■		■	■	■	■	■	■			■	■	9
Selenidera maculirostris			■	■	■		■	■	■		■	■	8
Turdus rufiventris			■	■	■	■	■	■		■	■		8
Dacnis cayana	■		■	■	■				■	■	■		7
Procnias nudicollis		■	■		■		■	■			■	■	7
Ramphastos vitellinus	■	■			■	■		■		■	■		7
Trogon rufus	■	■	■		■				■	■	■		7
Coereba flaveola	■	■	■						■	■	■		6
Myiodynastes maculatus	■	■	■							■	■	■	6
Phylloscartes oustaleti		■	■		■					■	■	■	6
Celeus flavescens			■			■		■		■	■		5
Cnemotriccus fuscatus		■	■							■	■	■	5
Euphonia violacea			■		■	■				■	■		5
Pachyramphus polychopterus		■	■				■	■			■		5
Ramphastos dicolorus			■		■	■				■	■	■	5
Tangara ornata			■		■		■	■				■	5
Chlorophanes spiza			■		■		■				■		4
Chlorophonia cyanea						■	■			■		■	4
Mionectes rufiventris			■				■			■	■		4
Oxyruncus cristatus		■	■						■			■	4
Patagioenas plumbea				■		■	■		■				4
Pyroderus scutatus			■		■					■	■		4
Syristes sibilator							■	■	■		■		4
Attila rufus			■			■					■		3
Carpornis cucullata					■	■	■						3
Elaenia sp1			■	■	■								3
Lathrotriccus euleri										■	■	■	3
Pachyramphus castaneus							■	■		■			3

Species	jan	feb	mar	apr	may	jun	jul	aug	sep	oct	nov	dec	Total
Pachyramphus viridis		■					■				■		3
Patagioenas cayennensis										■	■	■	3
Tangara palmarum			■			■	■						3
Tangara sayaca			■				■			■			3
Tityra cayana			■							■	■		3
Vireo olivaceus			■							■	■		3
Aburria jacutinga					■				■				2
Cyanocorax caeruleus					■	■							2
Elaenia obscura			■		■								2
Legatus leucophaius										■		■	2
Megarynchus pitangua			■							■			2
Orchesticus abeillei					■							■	2
Penelope obscura							■	■					2
Penelope superciliaris					■					■			2
Pipraeidea melanonota							■			■			2
Tersina viridis											■	■	2
Tityra inquisitor										■	■		2
Hemithraupis guira					■								1
Patagioenas picazuro										■			1
Pitangus sulphuratus										■			1
Saltator fuliginosus										■			1
	21	**25**	**46**	**22**	**39**	**29**	**36**	**29**	**26**	**46**	**46**	**31**	

Online Resource 9





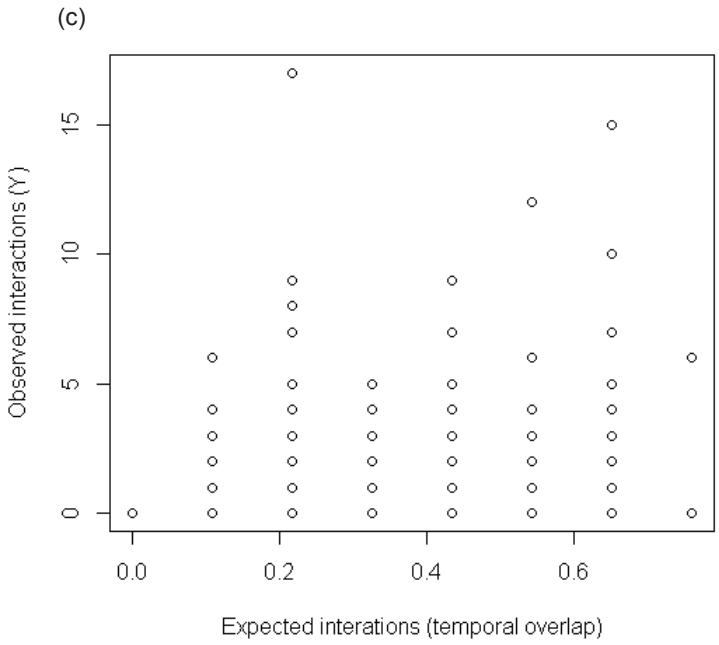


Figure S6. Fit of the observed interaction network (Y) to the model T. (a) Number of visits (circles sizes) of the observed seed dispersal interactions in Guaraqueçaba, southern Brazil (above) and (b) the probability of interactions from the temporal overlap model (below). Rows represent fruit-eating birds species and columns represent plant species. (c) The relationship between observed species pairwise interactions and expected interactions from temporal overlap model (T), calculated as the product of the interaction probabilities from T model and the total number of visits (n = 910).

Online Resource 10

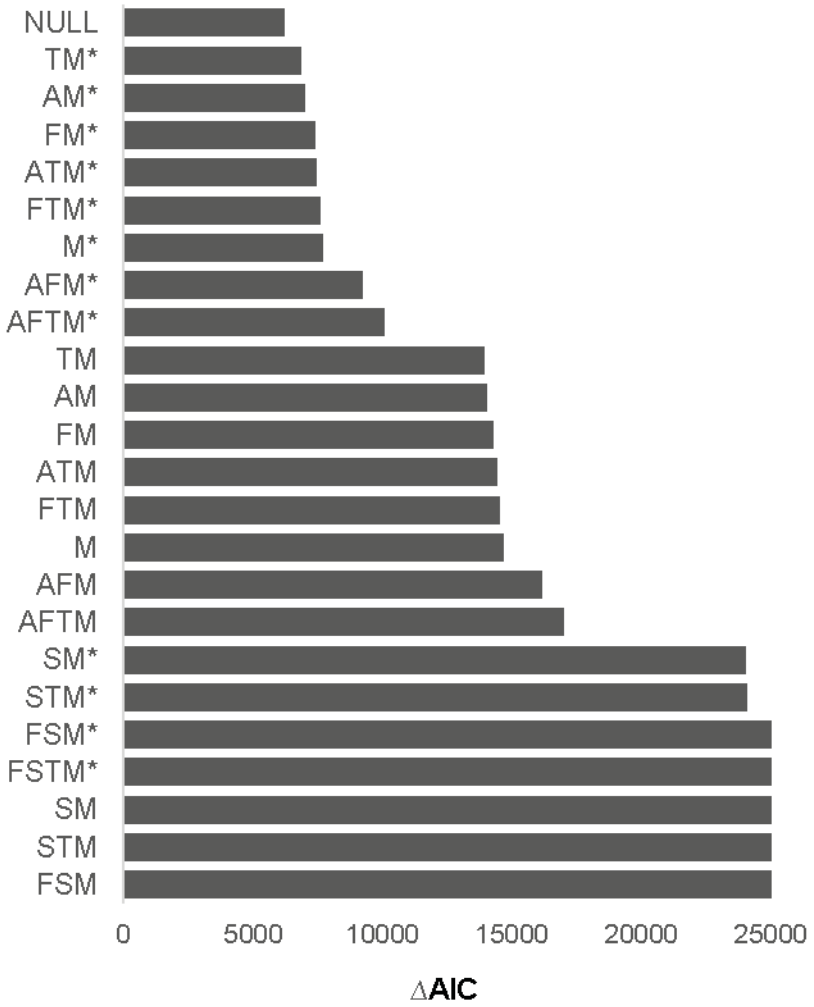


Figure S7. Microstructure predictive power of all models containing morphological barrier considering seed width (M*), with the models considering fruit width (M). The probability matrices were built based on relative species abundance (A), fruit production of plants and relative abundance of birds (F), spatial overlap (S), temporal overlap (T), morphological barrier considering seed width (M*), morphological barrier considering fruit width (M) and all possible combinations among these models. Null is the model in which all pairwise interactions have the same probability.

4 CAPÍTULO 2

AVES DISPERSORAS CENTRAIS TEM UM PAPEL IMPORTANTE NA MANUTENÇÃO DA DIVERSIDADE FUNCIONAL DE PLANTAS EM UMA REDE DE DISPERSÃO DE SEMENTES

Capítulo formatado de acordo com as normas do periódico: *Functional Ecology*

Central fruit-eating birds play a core role to the maintenance of functional diversity of plants in a seed dispersal network

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Summary

1. Central species play important roles maintaining the biodiversity, dynamics and stability of ecological networks since they interact with many species and present a relevant position on the network structure. However, the relevance of central species for the maintenance of the functional diversity in ecological networks remains little known.
2. Here, we introduced the concept of functional diversity of partners in ecological networks. We analysed the relationship between the functional diversity of partners and the centrality of fruit-eating birds in a seed dispersal network in the Brazilian Atlantic Forest. Given the importance of central species, we also evaluated the factors underlying the centrality of the fruit-eating birds, specifically abundance, level of frugivory, body mass, gape width and foraging strata.
3. Given the tendency of phylogenetically related species to present similar traits, we analysed the relationship between functional diversity of partners and the centrality of birds, as well as the mechanisms underlying the centrality, considering the phylogenetic relationship of species.
4. We found strong positive correlation between the centrality of fruit-eating birds and the functional diversity of plants with which they interact. Besides that, we identified that bird centralities were mostly related with species abundance, followed by the level of frugivory and ground-foraging.

5. Our findings reveal that central species of fruit-eating birds are important for the maintenance of functional diversity of bird-dispersed plants and ecosystem functions. Furthermore, the higher abundance of central fruit-eating birds increase the robustness of the seed dispersal network, once abundant species usually are less prone to extinction. Finally, we consider that the approach of functional diversity of partners introduced here may advance the understanding of the functional role of species in ecological networks and ecosystem function.

Key-words: centrality, ecological networks, ecosystem function, frugivory, functional traits, mutualism, mutualistic networks, phylogenetic relatedness, phylogenetic uncertainty, plant-animal interaction

Introduction

In the web of life, different species may play different roles (Paine 1969). Several studies have showed that centrality is an important facet of the role of species in ecological networks (e.g. Albert, Jeong & Barabási 2000, Memmott, Waser & Price 2004; Campbell et al. 2012; Palacio, Valderrama-Ardila & Kattan 2016). Central species are characterized by the higher number of interactions and by the relevant position, based in their interactions, within the structure of a network (Jordán, Liu & Daves 2006; Dormann 2011; González, Dalsgaard & Olesen 2010; Mello et al 2015). Indeed, the removal of central species of networks leads to loss of biodiversity (Cambell et al. 2012), destabilization and rupture of the network (Albert, Jeong & Barabási 2000, Memmott, Waser & Price 2004; Campbell et al. 2012; Palacio, Valderrama-Ardila & Kattan 2016). Thus, central species play important roles maintaining the structure and stability in ecological networks.

The centrality of species may be determined mainly by three different indices: degree, closeness, and betweenness (Freeman 1979). Degree centrality is the simplest measure of centrality and represents the number of interspecific interactions (i.e. links) made by a given node (Freeman 1979). Closeness centrality measures the proximity (the average length of the shortest path between the node and all other nodes in the graph) of a given species to all other species at the same level in the network (e.g. dispersers in a seed dispersal network) (Freeman 1979, Mello et al. 2015). In ecological terms, a central species (e.g. seed dispersers) has high closeness centrality when it shares partners (e.g. plant species) with many other species in a network, and it has low closeness centrality when its diet is more exclusive (Mello et al 2015).

Betweenness centrality measures the number of shortest paths between all pair of species of the same level (e.g. dispersers in a seed dispersal network) going through the focal species. Thus, betweenness describes the importance of species as connectors in a

given network (Freeman, 1979). In other words, species with high betweenness indirectly connect species of the same assemblage (e.g. fruit-eating birds) through their shared partners (e.g. plant species). Thus, considering the role of species for network structure, species may act as a hub (closeness centrality), sharing many partners with other species of the same assemblage, and/or as a connector (betweenness centrality) sharing partners with many species that do not share a common partner with each other (Freeman 1979; Mello et al. 2015).

Despite the known structural of species with high centrality, the role of central species for the maintenance of functional diversity in ecological networks remains little studied. Intuitively, the high closeness and/or betweenness of central species suggest that they are able to interact with species with different traits, since they share partners with many other species and/or connect species of different parts of the network. Therefore, the functional diversity of partners with which interacts should be high. Furthermore, this relationship must be stronger for species with high betweenness centrality since these species connect species of different parts of the networks, which are expected to be more functionally variable. In these cases, central species are important not only for the dynamics and stability of ecological networks but have an enhanced importance for the maintenance of functional diversity of species in ecological networks and ecosystems functioning.

Considering the functional roles of central species, we introduce in this study a concept and framework to measure the functional diversity of partners. For this end, we used a study case of seed dispersal network of the Brazilian Atlantic Forest. Seed dispersal interactions have been widely recognized as a key ecological function playing an important role in forests maintenance and conservation in most ecosystems (Jordano et al. 2011). This importance of seed dispersal interactions is accentuated in Neotropical

forests, where about 25 to 30% of birds include fruits on their diet (Pizo and Galetti 2010). Particularly, in biomes like the Brazilian Atlantic Forest, up to 90% of plant species may be dependent on seed dispersal by vertebrates and almost 40% of these plant species are dispersed exclusively by fruit-eating birds (Almeida-Neto et al. 2008).

Despite the importance of species with high centrality and seed dispersal interactions, few studies have addressed the mechanisms underlying the centrality of fruit-eating birds (e.g. Mello et al. 2015). Theoretically, all the characteristics that favor a species to interact with a large number of partners may define the species centrality. For seed dispersal networks, the level of frugivory (i.e. the proportion of fruits on diet) was already reported as an important factor to explain species centrality (Mello et al. 2015). However, others factors considered important for plant-animal interaction establishment, such as abundance (chapter one of this PhD thesis, Vázquez et al 2009), body mass (Fleming 1991), foraging strata (Schleuning et al. 2011) and gape width (Wheelwright 1985; Moran & Caterall 2010; Eklöf et al. 2013), may also influence the centrality of species. Nevertheless, the importance of these factors to define species' centrality in seed dispersal networks remains unknown.

Since more abundant species tend to interact more and with more partners (Vázquez 2005; Vázquez et al. 2007), the abundance of birds is expected to determine centrality. Body mass also has shown to be an important trait driving of centrality in fruit-eating birds in seed dispersal networks (Palacio et al, 2016), ants in ant-plant mutualistic networks (Chamberlain & Holland 2008) and food webs (Woodward et al. 2005). Moreover, the gape width of birds has also been pointed out as an important bird trait driving plant-bird interactions (Wheelwright 1985; Moran & Caterall 2010; Eklöf et al. 2013) since it is strongly correlated with seed and fruit size consumed by birds (Wheelwright 1985). Therefore, birds with large gape width may interact with a wide

range of seed sizes and consequently with a large number of plant species, what may increase its centrality. Additionally, the foraging strata may be also important, since frugivorous birds have been reported to be less specialized in the canopy stratum than in the midhigh and/or forest understory (Schleuning et al. 2011). Therefore, bird species that forage on the canopy interact with more plant species that may result in a higher centrality.

For fruit-eating birds, phylogenetically closely related species tend to show similar traits (Pigot et al. 2016). The non-independence of species traits associated to phylogenetic relatedness (Symonds & Blomberg 2014) highlight the importance to consider the phylogenetic relatedness when comparing species traits (Grafen 1989; Symonds & Blomberg 2014), as roles in networks and functional traits. Therefore, here we tested the relationship between the centrality of fruit-eating birds and the functional diversity of their mutualistic partners on a seed dispersal network at the Brazilian Atlantic Forest, taking into account the phylogenetic relatedness of fruit-eating birds. We expect a positive correlation between the centrality and the functional diversity of partners of fruit-eating birds.

Moreover, we also examined the mechanisms underlying the centrality of fruit-eating birds in our seed dispersal network, also taking into account the phylogenetic relatedness of the species. We expected a positive correlation among the centrality of fruit-eating birds and abundance as well as species traits as mentioned before (the proportion of fruits on diet, gape width, body mass and canopy-foraging). Finally, we discuss our findings highlighting the importance of considering the approach of functional diversity of partners to the knowledge about species roles in ecological networks and ecosystem functioning.

Materials and Methods

STUDY AREA AND SAMPLING DESIGN

We carried out the study in the northern coast of Paraná, Brazil (Atlantic Forest *stricto sensu*, 25º 10´ - 25º 14´ S and 48º 17´ - 48º 27´ W), at the protected areas Reserva Natural Papagaio-de-cara-roxa and Reserva Natural Salto Morato. The regional average annual temperature vary between 19ºC-21ºC and an average annual precipitation of 2403 mm (Vanhoni & Mendonça 2008).

We conducted the interaction observations on field work from April 2011 to October 2012 in 48 plots of 100 x 10 meters (0.1 ha) each. Plots encompassed a range of successional stages (from 18 to almost 100 years old post-disturbance forests that suffered either clear-cut or selective logging) and altitudes (from 20 to 270 meters a.s.l), reflecting the landscape heterogeneity of the northern coastal forests of Paraná (Kauano et al. 2012). In this way, we constructed a regional bird-seed dispersal network which includes all forest habitats available and the variation due to plot age (see Devoto et al. 2011 for a similar approach). We sampled 8 to 13 plots in a day for about 10 hours per day. We sampled each plot once a month. All bird-dispersed plants species observed were included. In each sampling, two observers registered the interactions between plants and fruit-eating birds. We observed three individuals for each fruiting species for at least 10 minutes. After 10 minutes, observations continued until all bird individuals recorded during the census had left the plant. When three individuals of a given plant species were not available, we extended observation time until a comparable sampling effort among species was achieved. We sampled the plots in a way that after one sampling day, each plant species with fruits had been observed an average of one hour per day.

We did not include the interactions with seed predators bird species (e.g. Psittacidae), as well as those birds that did not swallow the seeds (i.e. pulp-pecking birds)

or fruits were eaten piecemeal. Based on interaction records, we built a quantitative interaction matrix (Y = [y_{ij}]) with rows and columns corresponding to bird-dispersed plants and fruit-eating bird species, respectively. Each cell y_{ij} contained an integer representing the number of consumed fruits of a given plant *i* by a given bird *j*. We estimated sampling completeness of interactions based on the Chao 1 estimator of interaction richness following Devoto et al. (2012).

FUNCTIONAL TRAITS AND ABUNDANCE OF FRUIT-EATING BIRDS

We described each fruit-eating species according to four functional traits related with interactions with plants: gape width (mm), body mass (g), level of frugivory (percentage of fruit on diet), foraging strata (estimate percentage of foraging on ground, understory, midhigh and canopy). Gape width, i.e. the external distance between commissural points, was measured from birds captured in mist nets during field work. For the species that were not captured on mist-nets, we measured gape width from specimens from the Museu de História Natural Capão da Imbuia or taken from literature (for references see Database S1, Supporting information). Body mass, level of frugivory and foraging strata traits of species were taken from the Elton Traits database 1.0 (Wilman et al. 2014).

We estimated bird species abundance from fixed radius point censuses (adapted from Bibby et al.1992) for every 48 plots (100 x 10 m). We sampled bird abundance in six months from October 2011 to May 2012, except for January and April due to rainy weather. In each month sampled, we sampled bird abundance in eight plots each day, for six days, randomizing the order of plot sampling. Thus, we sampled each point census once per month of sampling. We remained 10 minutes in each point and recorded each bird seen or heard within a radius of 50 meters. To estimate the abundance of bird species we calculated the index of point abundance (IPA) for each species dividing the sum of

records for each species by the number of points sampled (n = 288), *i.e.*, the number of points (n = 48) multiplied by the sampling months (n = 6) (Vielliard et al. 2010).

FUNCTIONAL TRAITS OF PLANTS

We described the bird-dispersed plants using five functional traits related to the interaction with fruit-eating birds and/or ecosystem functioning: seed width, the colour of diaspore, type of diaspore, life form and maximum height of the plant. From the perspective of fruit-eating birds, seed width reflects the maximum size of a fruit that a bird can swallow and disperse (Wheelwright 1985). On the other hand, seed width is also an effect trait of ecosystem functioning being mainly related with seedling longevity (Saverimuttu & Westoby 1996) increasing the survival during seedling establishment (Dalling & Hubbell 2002, Westoby et al. 2002). Colour and type of diaspore are related with fruit detection and fruit choice by birds (e.g. Fisher & Chapman 1993, Cazetta, Schaefer, & Galetti, 2007; Flörchinger et al. 2010, Valido et al. 2011, Galetti, Pizo & Morellato 2011, Gagetti, Piratelli & Piña-Rodrigues 2016). Life form and maximum height of plants are related with the forest structure, fruit choice by birds (Flörchinger et al. 2010), and foraging strata of fruit-eating birds (Schleuning et al 2011). Moreover, maximum height of plants also describes spatial vegetation structure (Bourgeron 1983), which may also be related to the stratification of resources and habitat availability for animals (Ulyshen 2011).

To estimate mean seed width, color and type of diaspore for each plant species, we collected data on three individuals of each species, whenever possible, and we measured 10 seeds per individual. When we could not find three individuals, we collected more seeds from each individual to sum up 30 seeds. We measured seed width with the *software* Image J from images of seeds displayed on graph paper with millimetric scale.

Regarding maximum height, we get each species' values from the open TRY dataset (Kattge et al. 2011; https://www.try-db.org).

STATISTICAL ANALYSES

Centrality metrics of fruit-eating birds

Initially, we calculated the different unweighted measures of centrality from the functions 'DC', 'CC' and 'BC' in *bipartite* package of R statistical software (R Core Team 2017). Then, we tested the multicollinearity among the measures of centrality. We found strong Pearson correlation among the measures of centrality (DC ~ CC = 0.77; DC ~ BC = 0.93; CC ~ BC = 0.85). For example, the seven species with highest BC also were among the seven species with highest DC and the five with highest CC. From this, we decided to work only with betweenness centrality (measured from the function 'BC' in *bipartite* package) since this metric provides a conceptual information more appropriate for our interest and hypothesis (i.e. the focus on species acting as connectors), as addressed in the introduction. Therefore, given the strong correlation among the centrality indices, from now on we will refer to betweenness centrality only by the term centrality.

Functional diversity of partners

Here we present a conceptual and analytical framework on how to measure the functional diversity of partners. Conceptually, a given species with a high functional diversity of the mutualistic partners interact with species functionally distinct. Considering functional traits involved in bird-plant interactions, a given fruit-eating bird with high functional diversity of partners interacts, for example, with both plants with large seed and plants with small seeds, and/or interact with a wide variety of fruit colors, plant life forms (from herbaceous to tree plants). Thereby, we adapted the conventional measurement of

functional diversity of sites based on functional traits of species from the function 'dbFD', package *FD* of R statistical software (R Core Team 2017). We replaced the matrix of species abundances (rows) in sites (columns) for a matrix with the frequency of interactions between fruit-eating birds (rows) and bird-dispersed plants (columns) on the argument "*a*" of the function. Thus, implementing a matrix of functional traits of plants as argument "*x*" in the function 'dbFD', the outcome is the respective functional diversity obtained from the plant traits, weighted by the frequency of interaction of plants that each bird interacted. In other words, the outcome is the functional diversity of partners (plant species) for each fruit-eating bird.

From this approach, it is also possible to explore the many facets of functional diversity in the context of ecological networks. For example, it is possible to measure the functional dispersion (Laliberté & Legendre 2010), functional divergence and functional evenness (Villéger et al. 2008) of partners. Since we were interested in the range of plant functional traits covered by each bird, we focused our analysis on functional richness metric, which we called of functional richness of partners (FRp). However, given the fact that the functional richness is an important measure of functional diversity (Villéger et al. 2008), in many cases we will refer to the functional diversity as a proxy for more restrict concept of the functional richness, which was the metric evaluated in this study.

Relationship between functional richness of partners and betweenness centrality

To control the potential non-independence of residuals by phylogenetic relatedness we used a Phylogenetic Generalized Least Squares (PGLS) analysis (Grafen 1989; Symonds & Blomberg 2014). Therefore, we built a PGLS with FRp as response variables and betweenness centrality as predictor variable with expected covariance under a Brownian model (Felsenstein 1985, Martins & Hansen 1997) and a model fitted by maximizing the log-likelihood (Maximum-likelihood). Given the absence of a phylogenetic megatree of

birds with high support, as well as the bias of the use of consensual trees for not considering the variation between trees (Rubolini et al. 2015), we choose to work with phylogenetic uncertainty (Rangel et al. 2015; Huelsenbeck, Rannala & Masly 2016). We accounted for phylogenetic uncertainty because it provides more reliable parameter estimates and realistic confidence intervals in regression models (Rubolini et al. 2015). Therefore, we used a set of 1000 trees with different phylogenetic hypothesis from Hackett et al. (2008) generated by http://birdtree.org/ (Jetz et al. 2012) to obtain parameter estimates with very small (< 0.15%) coefficients of variation (Rubolini et al. 2015). In order to show the broad pattern of the regressions when considering the 1000 phylogenetic hypothesis, we calculated the mean intercept and estimate of betweenness for the PGLS models with a p-value of estimate < 0.05, and we ploted the mean line regression.

As suggested by Symonds and Blomberg (2014), we also used the method of (restricted) maximum likelihood (REML) to simultaneously fit the regression model and estimate λ (mean for the 1000 models) in a regression context, which represents the phylogenetic signal in the residuals. The estimate λ tests for the extent to which closely related species tend to resemble each other taking into account the relationship between the predictor variables and response. A λ value of 0 is consistent with no phylogenetic signal in the evolution of traits (independence of residuals or "star" phylogeny), whereas a value of 1 is consistent with strong phylogenetic signal following the Brownian motion model of evolution (Symonds & Blomberg 2014). The Brownian motion model assumes that changes in the value of a trait over a certain period is given by a random number drawn (random walk process) (Symonds & Blomberg 2014). Thereby, species that share a more recent common ancestor should have more similar trait values than more distantly related species because their traits have had less time to diverge (Symonds and Blomberg

2014). However, there is no clear-cut interpretation of whether intermediate values of λ indicate 'weak' or 'strong' phylogenetic signal in the residuals of the regression (Symonds & Blomberg 2014). Then, we made direct hypotheses tests by a likelihood ratio χ^2 test (LR) and calculate *P* values to compare, for each tree, whether the estimated maximum likelihood value of λ differs significantly from a model forced to have λ = 0 (independence of residuals or "star" phylogeny) or λ = 1 (Brownian motion model). Therefore, considering each tree, we ran likelihood ratio χ^2 test 1000 times for λ = 0 and 1000 times for λ = 1.

We performed all PGLS analyses on R statistical software (R Core Team 2017). We tested the assumptions of PGLS models checking the normality of residuals (Shapiro–Wilk test) for the 1000 models (one for each tree) and by the quantile-quantile plot of 100 random models. The assumption of homogeneity of residuals was checked by plotting the residuals of 100 random models against its fitted values. To measure the FRp we implemented the functional matrix with plant traits (matrix *x*) and interaction matrix (matrix *a*) in the function 'dbFD' in Package *FD* version 1.0-12. To evaluate the PGLS we used the 'gls' function and for the likelihood ratio χ^2 test we used the 'anova' function. Both functions belong to *nlme* package version 3.1-131.

Factors underlying betweenness centrality

We also built a PGLS with betweenness centrality as response variables and species traits, gape width, body mass, the percentage of fruit on diet, the percentage of foraging on ground, understory, midhigh and canopy strata, as predictor variables. First, we standardized the predictors by mean 0 and standard deviation 1. Then, we tested the multicollinearity of predictors using variance inflation factors (VIF). All categories of foraging strata showed high values of VIF (bigger than 10). Since the boundaries between understory and midhigh are subjective, we merged these foraging strata adding their

values in one category called under-midstory solving the problem of variance inflation among the predictors. Thereby, all predictors showed values of VIF lower than 2.

We ran the PGLS analyses considering the 1000 phylogenetic hypothesis of birds obtained from Hackett et al. (2008) generated by http://birdtree.org/ (Jetz et al. 2012). Taking into account the existence of biologically plausible hypotheses for all combinations of the predictor variables, we built the global model for each tree with all response variables. Then, we evaluated the model selection from all possible combinations of predictor variables using the function *dredge* of the package *MuMIn*. For each phylogenetic hypothesis, we selected models with $\Delta AIC < 2$. Taking into account the 1000 phylogenetic hypotheses, we evaluated the frequency of occurrence of all selected models for all 1000 trees. Furthermore, we evaluated the frequency of occurrence that a given model presented Δ AIC = 0 for each of all trees. Thereby, among all models with Δ AIC < 2 for all 1000 phylogenetic hypothesis, we choose the most simple and frequent model with Δ AIC = 0 as the best model.

Thus, we ran this best model for each phylogenetic hypothesis and obtained the intercept value, estimate and *P* values of each variable to plot the regression lines in a diagram. In order to show the broad pattern of the regressions when considering the 1000 phylogenetic hypothesis, we also calculated the mean intercept and estimate for each variable considering the PGLS models with p-value of estimate < 0.05 and plot the mean line regression of each variable. We tested the assumptions of PGLS models checking the normality of residuals (Shapiro–Wilk test) for the 1000 models (one for each tree) and by the quantile-quantile plot of 100 random models. The assumption of homogeneity of residuals was checked by plotting the residuals of 100 random models against its fitted values. To evaluate the PGLS analyses we used the 'gls' function of the *nlme* package version 3.1-131.

Results

SEED DISPERSAL NETWORK

The seed dispersal network was composed by 90 plant species and 67 bird species (Database S1, Supporting information; FigS1. Supporting information).Among the 6120 possible interactions, 496 pairwise interactions were recorded, including 910 visits by birds and 6215 fruits consumed. The sampling completeness indicates that we recorded most interactions (98 %) in the community (Fig. S2, Supporting information). Among birds, *Turdus albicollis* was the species that consumed the highest number of fruits (n = 830), followed by *Tangara cyanocephala* (n = 488) and *Tangara seledon* (n = 385). The fruits consumed by these three species corresponded to 27% of all fruits consumed (for more details of species see Database S1). The plant species with the highest fruit consumption were *Miconia cinerascens* (n = 719), *Myrcia* cf. *glabra* (n = 644) and *Casearia sylvestris* (n = 637) representing 32% of total fruit consumption.

THE RELATIONSHIP BETWEEN BETWEENNESS CENTRALITY AND FUNCTIONAL RICHNESS OF PARTNERS

The five bird species with higher betweenness centrality were *Tangara cyanocephala* (BC = 0.0845), followed by *Chiroxiphia caudata* (BC = 0.0795), *Trogon viridis* (BC = 0.0787), *Turdus albicollis* (BC = 0.0782) and *Tangara seledon* (BC = 0.0711) (Fig 1; Database S1).The five bird species with higher FRp were *Turdus albicollis* (FRp = 0.408), followed by *Trogon viridis* (FRp = 0.389), *Trichothraupis melanops* (FRp = 0.375), *Thraupis cyanoptera* (FRp = 0.356) and *Chiroxiphia caudata* (FRp = 0.355) (Fig. 1; Database S1).

Our PGLS results showed that fruit-eating birds with higher betweenness centrality cover a greater FRp (mean $\beta = 3.93$, mean SE = 0.518, $p < 0.05$ in 98% of models) (Figure 2). In general, different phylogenetic hypotheses define slightly different regression lines that vary around the same mean (Figure 2). In contrast, some phylogenetic hypotheses (26 from 1000) generated skewed regression lines with inverse relationships between the variables (Figure 2). For 21 bird species, the functional richness of partners (FRp) was not calculated since those species interacted with only one or two species of plants (see Database S1). We then excluded these bird species from the PGLS analyses.

The mean value of λ was close to zero (mean $\lambda = 0.141$, max = 0.490, min = 0.0006) and remained between the confidence interval for all models (mean IC lower = -0.762, mean IC upper = 1.044). Thus, our models presented weak phylogenetic signal on residuals (almost independent residuals) of the regression of FRp against betweenness. Comparing if our models significantly differed from models that were forced to have $\lambda = 0$ (independence of residuals or "star" phylogeny) by the likelihood ratio χ^2, none of our 1000 models showed a significant difference ($P > 0.05$). However, when we compared with $\lambda = 1$ (Brownian motion model), all results were significant ($P < 0.05$). These results showed that the relationship of FRp to betweenness is evolutionarily labile and does not follow a Brownian motion model of evolution. Although our models showed weak phylogenetic signal on residuals when considering all species, it is possible to notice certain congruence between values of FRp and betweenness for some phylogenetically related species (Figure 3). For example, *Turdus* spp., *Tangara* spp., *Trogon* spp. and the subfamily Ilicurinae (*Chiroxiphia caudata* and *Ilicura militaris*) showed both high values of FRp and betweenness centrality.

MECHANISMS UNDERLYING BETWEENNESS CENTRALITY

Regarding the mechanisms underlying betweenness centrality, the model described by abundance, level of frugivory and ground-foraging strata was the most frequent model with $\Delta AIC = 0$ (370 of 1000) and the third among models with $\Delta AIC < 2$ (650 of 1000) on model selection considering the 1000 phylogenetic hypotheses (Table 1). Moreover, this is the simplest model and is contained in the other models considered on model selection (Table 1). The regression lines of each variable for each phylogenetic hypothesis indicated that more abundant and/or fruit dependent and/or ground-foraging species presented higher betweenness centrality (Fig. 4). The regression lines of abundance showed a stronger correlation with betweenness centrality (Figure 4a). On the other hand, the regression lines of the level of frugivory and ground-foraging showed skewed slopes in relation to data distribution (Figs. 4b and 4c). With the exception of some extremes, different phylogenetic hypotheses defines slightly different regression lines that vary along the same mean (Fig. 4).

The mean λ in the regression context (i.e. phylogenetic signal in the residuals errors) was low (mean $\lambda = 0.18$, max = 0.27, min = 0.12) and remained between the confidence interval for all 1000 phylogenetic hypothesis (mean IC lower = - 0.27, mean IC upper = 0.64). None of our 1000 models showed a significant difference compared to those that were forced to have $\lambda = 0$, by the likelihood ratio χ^2. However, when we compared to models with $\lambda = 1$, all results were significant ($P < 0.05$). Our models thus presented a weak phylogenetic signal on residuals (independent residuals), and the evolution among betweenness and predictors is labile and do not follow Brownian motion model of evolution.

Discussion

Our study shows that central fruit-eating birds in the seed dispersal network feed on and disperse plants with distinct functional traits. We also showed that central species of fruit-eating birds tend to be more abundant, more dependent on fruits in the diet and foraging on the ground, independent from the phylogenetic relatedness. Among these characteristics, the abundance was the most strongly related variable to betweenness centrality, meaning that abundant birds tend to play central roles as seed dispersers in the community. Therefore, besides the importance of central species for the structure, dynamics and stability of ecological networks (Albert et al. 2000, Memmott, J. et al. 2004, Campbell et al. 2012), here we showed that central fruit-eating birds are also important to maintain the functional diversity of bird-dispersed plants and, therefore, ecosystem functioning.

The strong correlation between FRp of fruit-eating birds and their BC indicates that central species interact with plants very distinct functionally. The positive correlation among the centrality indices of species was also found in previous studies of ecological networks (e.g. González et al. 2010; Encinas-Viso et al. 2014; Palacio et al. 2016). Thus, species that interact with a large number of partners can also act as both local hubs and connectors of the network and cover high FRp. Therefore, this structural and functional role of central fruit-eating birds enhance the importance of these species in seed dispersal networks and suggest that central species should receive high conservation priorities.

The weak phylogenetic signal found in the regression between FRp and betweenness centrality suggest that species roles in the network is not explained by the shared evolutionary history of them. However, some phylogenetically related species (e.g. *Turdus* spp., *Tangara* spp., *Trogon* spp. and the subfamily Ilicurinae (*Chiroxiphia caudata* and *Ilicura militaris*) presented both high centrality and functional diversity of

partners. For these clades, network roles seem phylogenetically conserved. However, this apparent phylogenetic signal in some terminal branches weakens when considering the whole phylogeny, resulting in the weak phylogenetic signal found in relationship between FRp and betweenness of all species.

We found that central species of fruit-eating birds tend to be more abundant, more dependent on fruits in the diet and foraging on the ground, independent from the phylogenetic relatedness. Indeed, studies showed that abundant species increased the probability to encounter a partner so they tend to interact with more partners presenting higher frequency of interactions (Vázquez 2005; Vázquez et al. 2007). However, we also showed that higher abundance also increases the ability of species to connect different parts of the network by betweenness centrality. This relationship was also found by previous studies considering simulations of populations size (Encinas-Viso et al. 2014). Moreover, the abundance of fruit-eating birds was the best mechanism underlying the microstructure (pairwise interactions) of other networks (Kaiser-Bunbury et al. 2014; Burns 2006). Considering the lower extinction risk of abundant species compared to rare ones (Pimm et al. 1988), the higher abundance of central species in the network increase the stability and robustness against cascade extinctions of mutualistic partners. However, there are many cases of once-abundant species that are today listed as endangered or extinct (e.g. *Emberiza aureola*, *Bombus affinis, Equus quagga*) alerting for the importance of also devote efforts for studies and conservation of abundant species.

Central fruit-eating birds presented a higher dependency on fruits. Thus, the need to interact with a wide range of bird-dispersed plants to fulfill their energetic requirements (Grass, Berens & Farwig 2014) seems to increase fruit-eating birds' centrality. Indeed, for both birds and bats, the level of frugivory is known to influence species roles in seed dispersal networks (Mello et al. 2015, Sebastián-González 2017) what reinforces the

importance of conserving obligate frugivorous birds. Although ground-foraging trait also explained species centrality, it is possible that this relationship have been influenced by *T. albicollis*. This species present the fourth highest value of FRp and second highest value of ground-foraging (Figure 4c). Based on our field observations, this species often forages on ground for invertebrates, as earthworms, spiders and insects, but not for fruits. In fact, all our records of fruit consumption for this species were perched on plants (never on the ground). Indeed, Gasperin and Pizo (2009) studying the frugivory and habitat use by thrushes (*Turdus* spp.) in south Brazil, found that most of the foraging records were on the ground, where birds got mainly invertebrates. Thus seems that the relationship between BC and ground-foraging for frugivory is not so trustworthy.

In sum, our findings highlight that, in addition to the importance of the structure and dynamics of seed dispersal networks, central fruit-eating birds are also important to the maintenance of plants functional diversity and, therefore, to ecosystem function of tropical forests. The fact that central species of fruit-eating birds tend to be more abundant and more dependent on fruits in the diet suggest that not only the conservation of obligate frugivorous must increase, but also the conservation of abundant species. In addition, the conceptual and analytical framework we propose to explore functional diversity of partners may generate new opportunities to understand the functional roles of species in the context of ecological networks and ecosystem function and to test the generalization of our findings to other communities and types of interactions (e.g. ant-plant interaction networks, pollination, host-parasite, trophic, etc.). Therefore, future studies evaluating the relationship of the functional diversity of partners with species properties in the interaction networks may advances the knowledge of ecological networks and the role of interactions in the functioning of ecosystems.

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Data accessibility

We intend to archive our raw data of interaction network, plant and bird abundances, productivity of plants, spatial overlap, temporal overlap, seed width and gape width of fruit-eating birds on Dryad Digital Repository.

Authors' contributions

TM-de-S and IGV conceived the ideas and designed methodology; TM-de-S collected the data, analyzed and wrote the first draft of the manuscript; IGV contributed substantially to revisions.

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Table 1. Regression models between betweenness centrality and the underlying factors (abundance, level of frugivory, gape width, body mass and foraging strata). The percentage values indicate the number of times that each model showed ΔAIC = 0 and/or ΔAIC < 2 among the 1000 models with different phylogenetic hypotheses evaluated.

Models	ΔAIC = 0	ΔAIC < 2
Betweenness ~ abundance + level of frugivory + ground	37%	65%
Betweenness ~ abundance + level of frugivory + ground + und-midstory + canopy	28%	69%
Betweenness ~ abundance + level of frugivory + ground + canopy	19%	68%
Betweenness ~ abundance + level of frugivory + ground + und-midstory	6%	55%
Betweenness ~ abundance + level of frugivory + ground + gape width	3%	56%

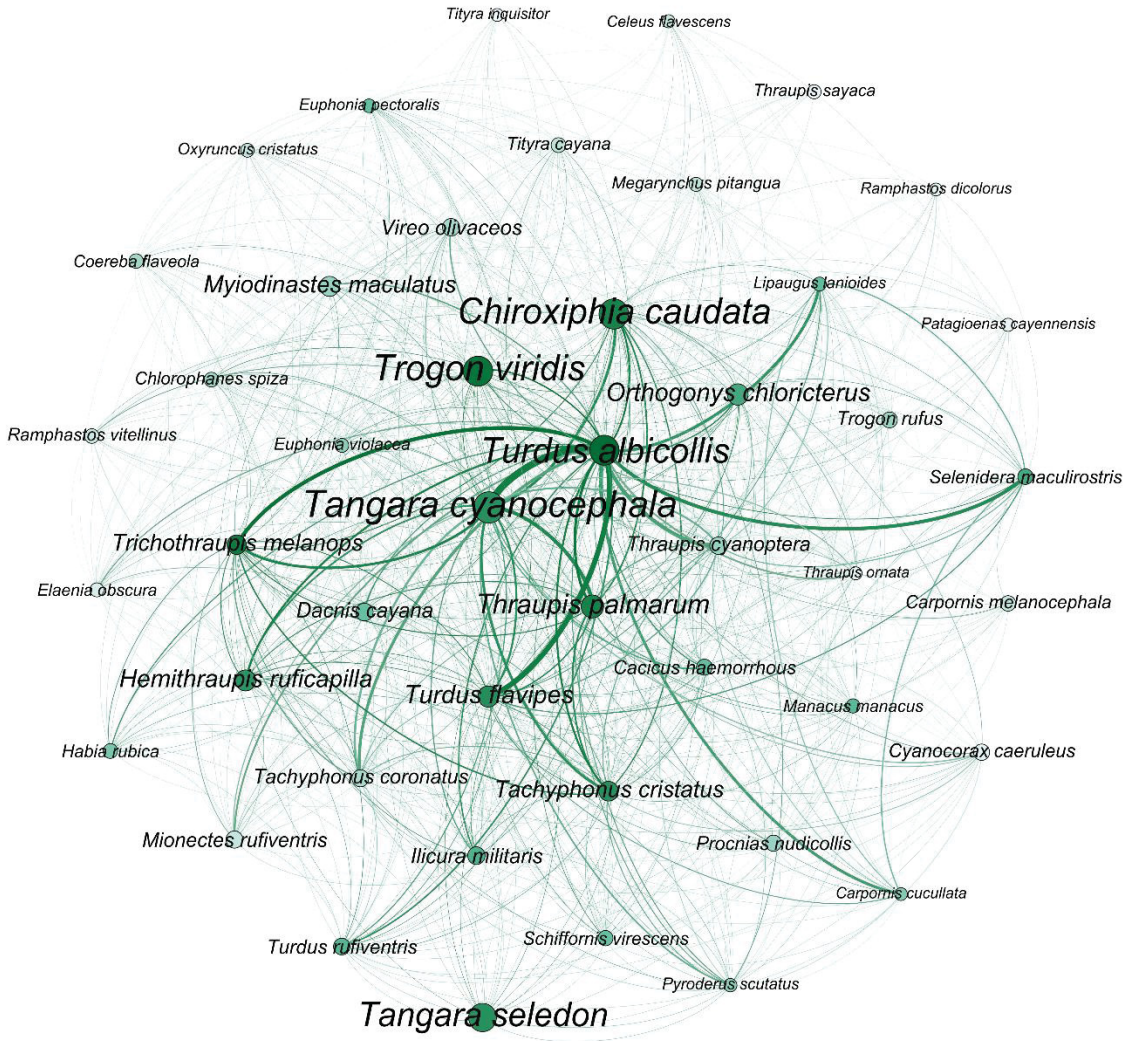

Figure 1. Unipartite fruit-eating birds network showing the betweenness centrality (larger nodes represent higher betweenness) and functional richness of partners (darker greens represent higher FRp). Label sizes are related to the node size (betweenness centrality).

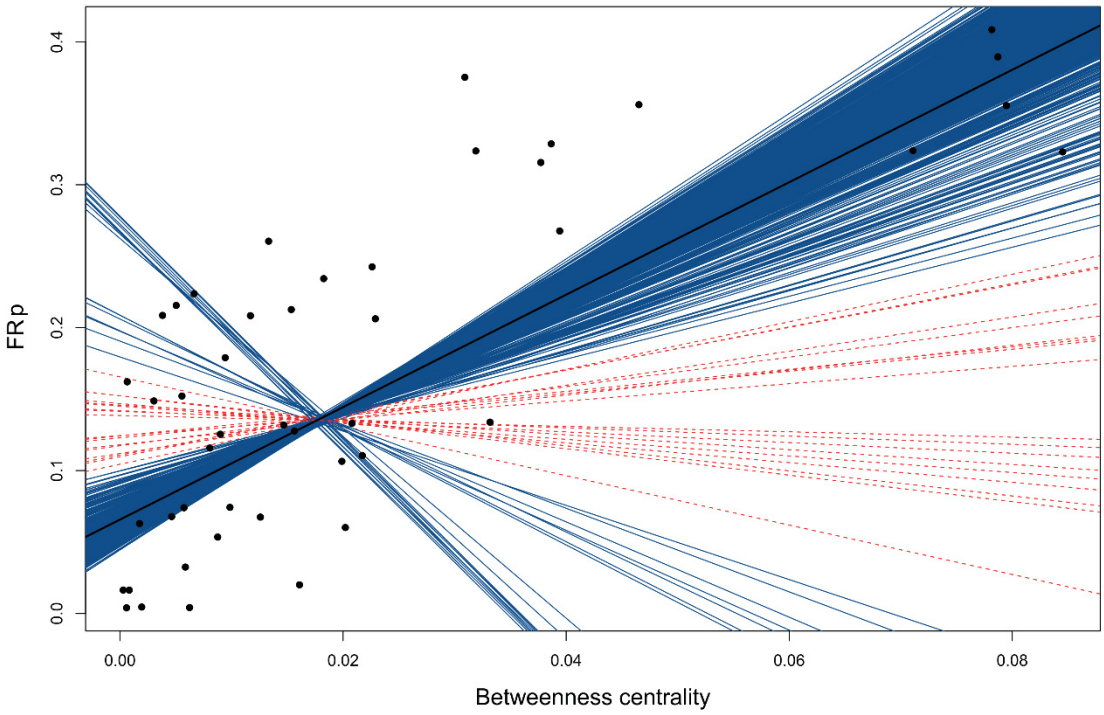

Figure 2. Regression lines of Phylogenetic Generalized Linear Squares (PGLS) of functional richness of partners against the betweenness centrality of fruit-eating birds. Each of 1000 regression lines corresponds to a phylogenetic hypothesis. Blue regression lines correspond to models with a significant estimate of betweenness ($P < 0.05$), while red regression lines correspond to a non-significant estimate of betweenness ($P > 0.05$).

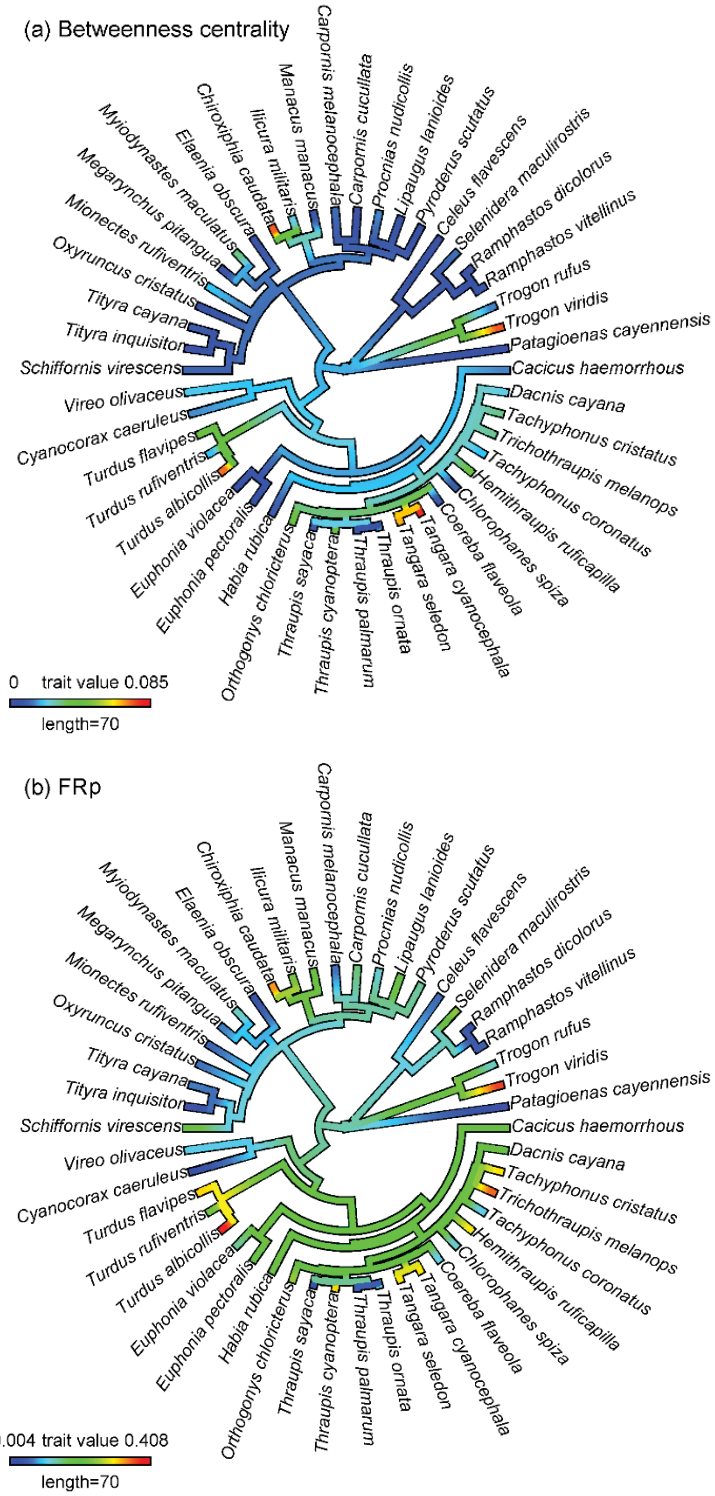

Figure 3. Values of (a) betweenness centrality and (b) functional richness of partners of species in a phylogenetic hypothesis randomly chosen.

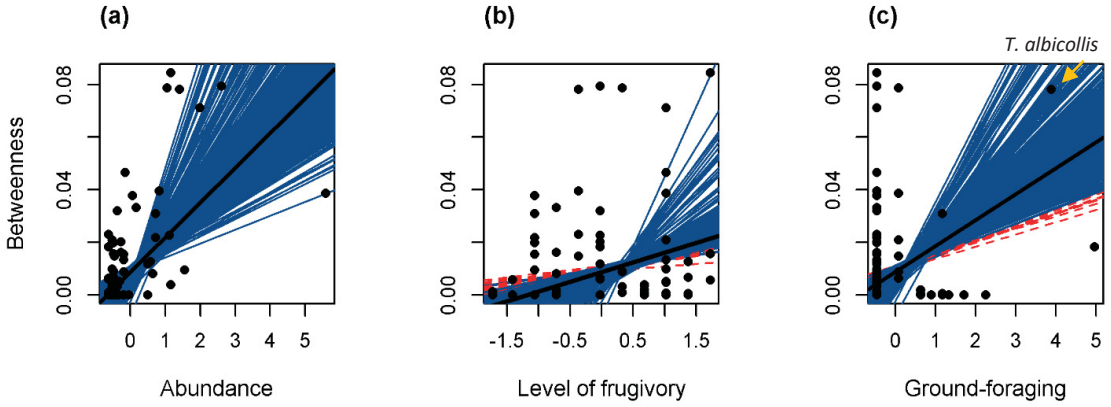

Figure 4. Regression lines of the best model of Phylogenetic Generalized Linear Squares (PGLS) of betweenness centrality against the fruit-eating birds (a) abundance, (b) level of frugivory and (c) ground-foraging. Each of 1000 regression lines in each diagram corresponds to a phylogenetic hypothesis. Blue regression lines correspond to models with a significant estimate of the variable ($P < 0.05$), while red regression lines correspond to a non-significant estimate ($P > 0.05$).

Supporting information

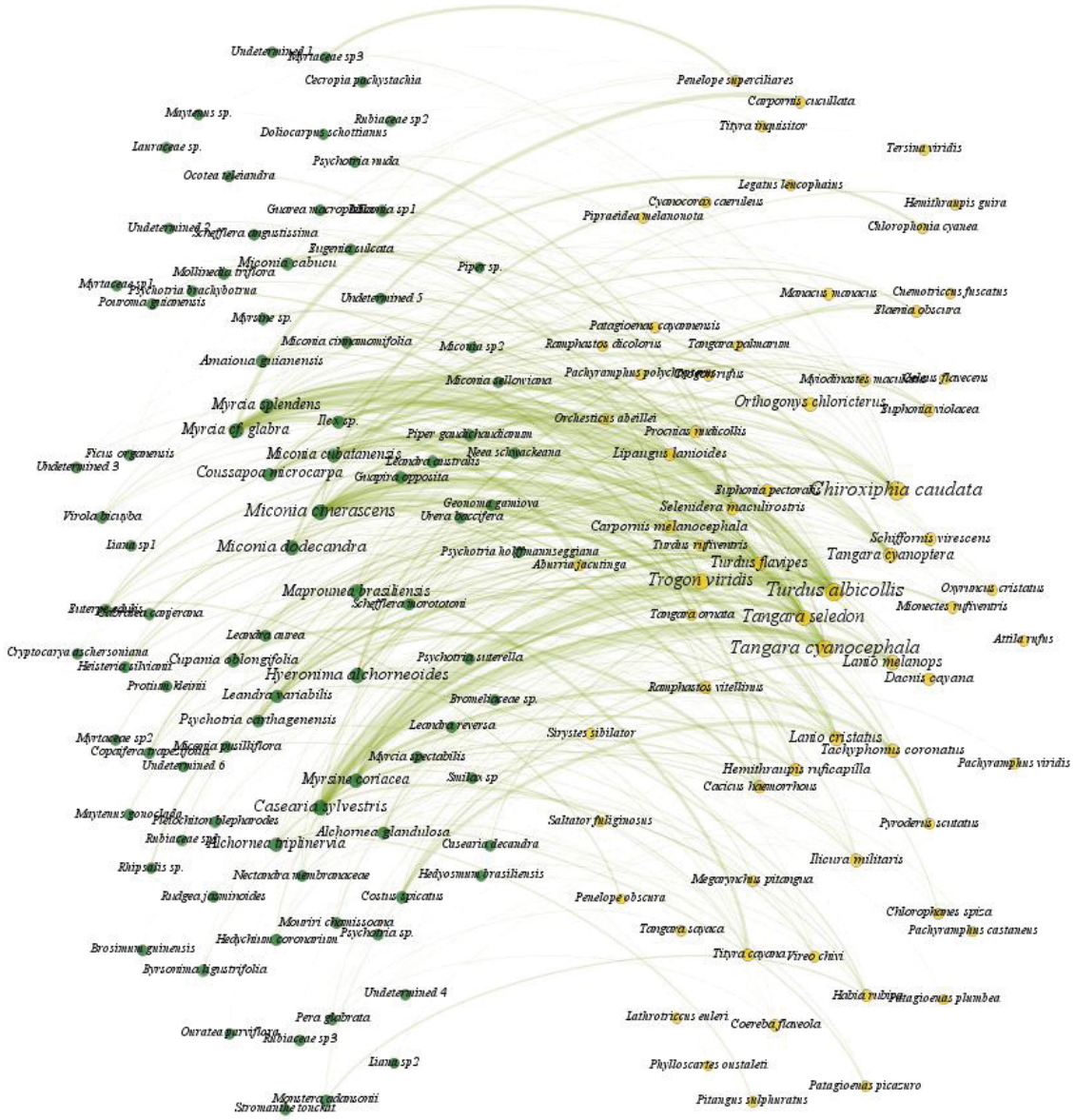

Fig. S1. Bird seed-dispersal network in the Atlantic Forest of southern Brazil. Plant species are on the left and bird species on the right. Lines represent species interactions and line thickness indicates number of fruits dispersed.

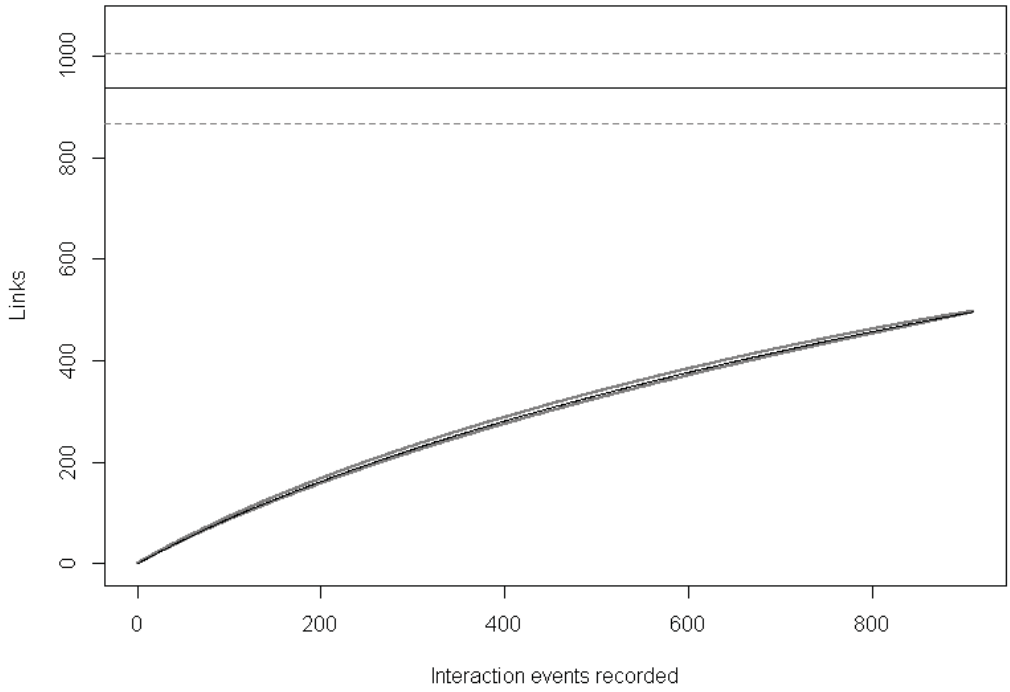

Fig. S2. Sampling completeness measure from rarefaction of unique interactions and interaction events (visits) for the observed seed dispersal network in the Atlantic Forest of southern Brazil. Horizontal black lines represent the Chao 1 estimate of asymptotic species richness with 95% confidence intervals (dashed lines).

5 CONCLUSÃO GERAL

Este estudo contribuiu para o entendimento dos processos determinantes de redes mutualísticas de dispersão de sementes. Embora uma combinação de processos neutros e baseados em nichos tenham sido bons preditores da estrutura geral da rede de dispersão de sementes de aves, um processo baseado em nicho (ou seja, sobreposição temporal) foi o melhor preditor da microestrutura da rede. Isto indica que as redes de dispersão de sementes podem ser fortemente influenciadas por alterações na fenologia de plantas e aves, principalmente aves migratórias ou que realizam deslocamentos altitudinais sazonais. Como a fenologia de plantas é afetada pelas mudanças climáticas, torna-se crucial que novos estudos incluam a avaliação do efeito das variações fenológicas ao longo do tempo nas interações entre plantas e animais. Ademais, uma questão bastante debatida em redes de interações ecológicas são as restrições impostas por interações proibidas devido a barreiras morfológicas. Assim, este estudo contribui com essa discussão evidenciando que o uso da largura da semente, ao invés da largura do fruto, deve ser preferencialmente considerado nas análises de compatibilidade ou barreira morfológica.

Outra contribuição importante deste estudo foi a implementação de uma nova forma de avaliar a medida de diversidade funcional de parceiros. A relação direta desta medida com a centralidade das aves dispersoras indica que espécies centrais podem ser importantes não só para a dinâmica e estabilidade de redes ecológicas, mas também para a manutenção da diversidade funcional nas redes e ecossistemas. Assim, esta abordagem permite avaliar o papel funcional das espécies nas redes e nos ecossistemas, pela perspectiva das interações, e poderá ser aplicada não só para redes de dispersão de sementes, mas também para os diversos tipos de redes ecológicas (e.g. redes de interação entre formigas e plantas, de polinização, parasito-hospedeiro, tróficas, etc.). Portanto, estudos futuros avaliando a relação das propriedades das espécies nas redes de interação com a diversidade funcional de parceiros, certamente trarão grandes avanços para o conhecimento de redes ecológicas e o papel das interações no funcionamento de ecossistemas.

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